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CONTENTS

No. 1, March, 1928

PAGE

The Sensory Capacities and Intelligence of Dogs, with a Report on the Ability of the Noted Dog "Fellow" to Respond to Verbal Stimuli ..... *C. J. Warden and L. H. Warner* 1
The History of Whales. Their Adaptation to Life in the Water. *Remington Kellogg* 29
Recent Developments in the Philosophy of Biology ..... *Joseph Needham* 77
Cephalopod Adaptations—The Record and Its Interpretation ..... *Edward W. Berry* 92
The Life Cycle and Mating Habits of the Male Tarantula ..... *W. J. Baerg* 109
New Biological Books:
Human Sapience ..... *Charles P. Winsor* 117
Brief Notices 127

No. 2, June, 1928

Homology, Analogy and Plasis ..... *John Tait* 151
The History of Whales. Their Adaptation to Life in the Water (Concluded) ..... *Remington Kellogg* 174
The Effect of Carbon Dioxide on Bacteria ..... *George Valley* 209
The Evolutionary Significance of the Protozoan Parasites of Monkeys and Man ..... *Robert Hegner* 225
Haldane on Selection ..... *Lowell J. Reed* 245
Seasonal Modifications in Testes of Vertebrates ..... *R. M. Oslund* 254
Evolution and Mortality ..... *Raymond Pearl* 271
New Biological Books:
Brief Notices 281

No. 3, September, 1928

The Gene ..... *Richard Goldschmidt* 307
Sub-human Culture Beginnings ..... *A. L. Kroeber* 325
Root Hairs and Growth ..... *Clifford H. Farr* 343
Controlled Mating in Honeybees ..... *Lloyd R. Watson* 377
Experiments on Longevity ..... *Raymond Pearl* 391
Criteria for Distinguishing Identical and Fraternal Twins ..... *Taku Komai* 408
New Biological Books:
Morgan on Entwicklungsmechanik ..... *S. R. Detwiler and H. B. Adelmann* 419
Brief Notices 427

No. 4, December, 1928

The Chloroplast Pigments, their Functions, and the Probable Relation of Chlorophyll to the Vitamines ..... *Frank M. Schertz* 459
The Development of Modern Comparative Psychology ..... *C. J. Warden* 486
Animal Evolution ..... *Austin H. Clark* 523
The Metabolism of Insects ..... *Mary Honora Sayle* 542

Social Parasitism in Birds.....*Herbert Friedmann* 554
New Biological Books:
Brief Notices..... 570
The Cost of Biological Books in 1928.....*Raymond Pearl* 600
Index to Volume III..... 605

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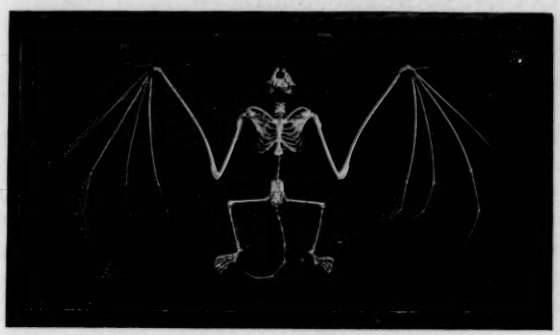

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VOL. III, No. 1 MARCH, 1928

THE QUARTERLY REVIEW of BIOLOGY

THE SENSORY CAPACITIES AND INTELLIGENCE OF DOGS, WITH A REPORT ON THE ABILITY OF THE NOTED DOG "FELLOW" TO RESPOND TO VERBAL STIMULI

BY C. J. WARDEN AND L. H. WARNER
Animal Laboratory, Department of Psychology, Columbia University

THE material selected for discussion in this paper naturally falls into two major divisions as indicated in the title. The attempt is made in the first general section to present, very briefly indeed, a fairly systematic account of the more important aspects of the capacities and behavior of the dog, insofar as these have been revealed by careful observation and experimental analysis. Vastly more information is at hand on the sensory capacities of the dog than on what we usually think of as general intelligence. The sections covering such capacities, especially visual, olfactory and auditory, are accordingly large while that on intelligence is correspondingly small. The distinction here made is, of course, one of convenience only, inasmuch as general intelligence must be, in the very nature of the case, a function of sensory and other capacities. A short section treating of the special fitness of the dog to serve as a subject for extensive and intensive behavior studies in the modern animal laboratory will follow that on intelligence. The second major division of the paper will consist of a fairly detailed account of certain tests, recently conducted by the writers, on the German Shepherd Dog "Fellow"—widely known on stage and screen—to determine to what extent, if any, his reputed ability to understand human language is justly warranted.

Before entering upon the main discussion it may be not entirely out of place to remind you that the attitude of the modern comparative psychologist is one of healthy skepticism toward supposed cases of animal genius and human-like levels of animal intelligence. It is not that the student of animal behavior has a grudge against the infra-human kind, or any scientific or philosophical objection to a high evaluation of their abilities. For, in point of fact, no one more than the comparative psychologist welcomes evidence tending to confirm his belief in the essential continuity of all living forms on the

mental, as well as the physical side. He merely insists more emphatically than formerly that evidences of this character must run the usual gauntlet of scientific criticism; that claims of this sort must first be established by the most painstaking and defensible scientific methodology.

Much of what the average man "knows" about his own dog, and about dogs in general is, of course, quite unknown to the animal psychologist. For no animal has a richer heritage of lore, sentimental and lofty, representing an accumulation of the long ages since primitive man first made the dog his hunting companion and his domestic ally. It is difficult for any of us to escape entirely this traditional influence; most difficult indeed to observe with clarity of purpose and uncompromising logic the behavior of a dog, or other pet, to which we have formed an attachment. Only a few decades ago, and even in certain circles now, the method of anecdote with its unfailing tendency toward anthropomorphic interpretation stood in high favor, and passed itself off under the guise of science. Selecting cases to bolster up a theory may be an interesting diversion but it is hardly worthy of the trained mind in any field. We have deliberately eliminated from the following discussion all anecdote and have meant to include only such observational and experimental results as appeared to us to be worthy of the attention of the serious scientist.

I. SENSORY CAPACITIES AND INTELLIGENCE

Visual capacity

Consideration of the experimental literature on the visual capacity of dogs indicates that the average dog has far more faulty vision than most dog-lovers suppose. Behavior evidence for this conclusion is supported by anatomical study of the eye. Slonaker (43) reports that the dog possesses no fovea and that even the so-called "sensitive areas" are only vaguely defined. Numerous opaque nerve fibres are said to penetrate the retina, and these must be considered as blind spots. The pupillary opening is always relatively large and the pupillary response, while rather quick, is not strong. Johnson (22) and others have demonstrated convergence.

The method ordinarily used in testing the dog's eyesight has been called the discrimination method, and in most cases involves the use of the original "discrimination box" designed by Yerkes and Watson (58), or some modification of this. The dog being tested is faced with a choice of two alleyways, the one leading to a compartment in which he will find food, the other to a compartment where he is usually given a light electric shock. Whether or not the dog makes a fortunate choice he is faced with this situation again and again. Sometimes the reward is to the right and the punishment to the left, sometimes just the reverse. The only way the animal can be sure of making a correct choice is by attending to signals or cues (stimulus patches) which are presented at the entrance of the alleyways. In testing for brightness discrimination, for example, a very bright light may be placed always at the entrance of whichever alley in that trial leads to the food, a less bright light at the other alley entrance. Many precautions must be taken to insure the fact that there are no other stimuli than the signals being studied which might give the animal a clue as to which alley to enter. Use of his nose to detect the side of the box at which he will receive food will not help the dog for there is food in both compartments, though in the punishment compartment it is screened off so as to be inaccessible. The experimenter must be entirely eliminated

from the situation, for the dog, more perhaps than any other animal, is quick to take advantage of the to us almost imperceptible movements that the onlooker often and quite unwittingly makes in indication of the correct direction.

This method has been used in the study of brightness, size, and form discrimination in the dog but not, as yet, in the study of color discrimination. Under adequate experimental conditions positive results as obtained by this method may be accepted as final, but it is to be noted that negative results cannot be considered conclusive, since it is conceivable that an animal might be capable of somewhat more delicate discriminations in a less arbitrary or complex situation.

Szymanski (51) used this general method in studying brightness discrimination. His dogs were a cross between a Spitz and a fox terrier. His results were entirely negative for slight differences in brightness. Only when one alley was brightly lighted and the other entirely dark was he able to get a discrimination habit. Very similar results were obtained by Sutherland (46) using the same method. His dogs, mongrels, discriminated between a light and no light, but not between one light as opposed to two lights, or even as opposed to four lights. Form as well as brightness discrimination would have been involved in these cases of course, since the bulbs were actually in view. Stone (45), however, using a male and a female fox terrier found evidence for a much finer degree of brightness discrimination. Having built up a discrimination habit for two lights differing considerably in brightness he gradually reduced the intensity of the brighter until a point was reached where the habit broke down. He then increased the difference between the two lights until the habit was reestablished and again gradually approached the threshold value. Stone also tested three human subjects by the same method —except, of course, that these subjects indicated by word of mouth rather than by turning to the right or left which light was in their opinion the brighter. The men could, on the average, distinguish a light of 1 c.p. from 1.1 c.p. The male dog discriminated between a 1 c.p. and a 1.2 c.p. light, while the female dog did slightly better. The dogs were thus inferior to the men, but only slightly so.

All the work on form and size discrimination except that of the Russian school is in accord with the conclusion that the dog is very deficient in these respects. Johnson (23), using an English bull terrier, was unable to establish evidence for discrimination between vertical and horizontal lines, these lines, alternately black and white, being 3.9 mm. wide on a circular field 6 cm. in diameter. Skiascopic examination of the dog's eyes, both with and without mydriatic, seemed to indicate that objects at a distance of twenty feet or more, i.e., at a distance such that the light rays were approximately parallel, were focussed on the retina. Nothing is known of the ability of the dog to accommodate, and thus it might have been that failure to discriminate in Johnson's case resulted from inability to focus upon objects so close to the eyes as the signals were placed. Johnson considered overcoming this difficulty by equipping the dog with a pair of spectacles. Instead, however, he introduced a system of lenses before the signals in such a way as to throw the light reflected from them onto the dog's eyes in parallel rays. But even with all these advantages that science offered the dog did no better. It could not even distinguish between a plain field and one of black and white stripes, 3.9 mm. in width. Each of these stripes subtended a visual angle of 33′ 32″ or an

angle larger than that subtended by the sun's disc at the earth. Johnson states that this coarsely striped field is "closely comparable with that of a plank fence, the units of which are 6 inches wide and 6 inches apart, viewed at a distance of 50 feet." Most dog-lovers would refuse to believe that their pets were incapable of such a discrimination.

Data on form vision have been reported by Williams (56) and by Szymanski (51). In neither case were the experimental conditions so admirably controlled as in Johnson's study. Williams was unable to establish discrimination between a square and a circle of equal area, although he did find discrimination between a constant and an intermittent light, the latter flashing at 2 second intervals. Szymanski was unable to establish response to a white pyramid standing in bold relief against a black background.

Johnson alone of American workers has studied size discrimination (22). His dog apparently discriminated between a circle 6 cm. in diameter and circles with diameters of 1, 2, and 3 cm. respectively. The 4 and 5 cm. circles were not certainly discriminated from the 6 cm. circle. The intensity of the light transmitted through the pairs of circles used was always constant. Thus it was impossible to say whether the animal's success was due to size discrimination or to luminosity. To test this matter Johnson equated the 6 and the 3 cm. circles for luminosity by reducing the larger circle to 25 per cent of its original brightness. As a result the dog no longer discriminated, choosing now one and now the other circle. His discrimination had therefore been based on luminosity differences.

The students of Pavlov, working in Leningrad, have reported data bearing on the sensory capacities of dogs. Unfortunately we are at present largely dependent on secondary source material, and thus a critical evaluation of the Russian work cannot readily be made. The method employed is quite different from that used by these other investigators, and the work still awaits verification in other laboratories. It involves the establishment of a conditioned salivary response to a given stimulus, as for example a black patch, by presenting this stimulus and the unconditioned stimulus, food, simultaneously a large number of times. After this conditioning is firmly established a second stimulus to be discriminated from the conditioned stimulus (a white patch, for example) is presented. Food is never presented with the white patch, whereas the black patch is often reenforced by the simultaneous presentation of food. Such training finally results in a differential response to the white and to the black patch, each presented alone, the one causing secretion of saliva, the other inhibiting such secretion, provided, of course, the sensory capacity of the dog is such as to permit such discrimination. Not only the visual capacity of the dog, but its auditory, olfactory, thermal, tactual, and gustatory capacities have been studied to some extent by this method. In general it may be stated that where the results of the Russian workers and those of other investigators are not in agreement, the findings of the former group seem to indicate greater sensory capacity. There are at least two possible explanations for these discrepancies. The salivary response method may be a more delicate measure of discriminatory ability involving, as it does, a more simple learning problem. On the other hand it may very well be that, due to technical errors in the application of the method, the dogs studied by the Russian students were responding to secondary criteria. That the latter is true of much of the

earlier Russian work seems evident. H. M. Johnson has subjected such studies to rigorous criticism. Partly as a result of such criticism, no doubt, radical changes have more recently been made in the technique employed by Pavlov's students. Whether or not these sufficed to entirely eliminate secondary clues cannot be said with our present indirect knowledge of their procedure. They have, apparently, succeeded in eliminating the experimenter from the situation, but this has necessitated the introduction of complicated mechanical devices for the presentation of the stimuli, which in themselves may conceivably offer secondary cues. It seems necessary, then, for us to present their results, largely on the basis of their report in Pavlov's recent volume, *Conditioned Reflexes* (35), with the hope that it will not be long until their experiments are known to us in greater detail and furthermore, have been verified in other laboratories.

Concerning the discrimination by the dog of intensity and luminosity differences the Russian work supports the results of Stone (45) mentioned above, who found greater acuity in this respect than any other investigator excepting the Russians. Frolov (35) using the Zimmermann series of grey papers, ranging from white to black, found the dog studied to be slightly superior to human beings, whereas Stone, using a different breed of dog, found them only slightly inferior to man. With respect to the discrimination of form and size, Orbeli reports results conflicting radically with those of other workers, since they seem to indicate discrimination of a large letter T from such forms as a square, a circle and so on. The luminosity and size factors, however, were apparently uncontrolled. It seems that the work on size discrimination must be thrown out on the same grounds. Furthermore, Orbeli's work was done in 1907 before the improved technique was introduced (57) in Leningrad. The work of Shenger-Krestovnikova (35) reported in 1921 cannot be criticised on the grounds of failure to control luminosity, since this investigator used figures constant in area and intensity, differing only in form. The two forms to be discriminated were a circle and an ellipse. At first an ellipse was used, the ratio of whose semi-axes was as 2:1. The discrimination was apparently made. This was followed by using a series of ellipses gradually approximating the circle in form. The ellipse whose semi-axes bore the ratio 9:8 proved to be the limit at which differentiation just failed. Returning to the flatter and longer ellipse, and reestablishing the discrimination for it, the threshold was again approached and with the same result. The indication is therefore for an acuity not far inferior to that of man. This conclusion is, however, not supported by any other modern work from the Pavlov laboratory so far as we know, and is, furthermore, contrary to the bulk of evidence from all other sources.

Can the dog see colors or is his visual world composed of only lighter and darker shades? The general opinion of animal psychologists, in the light of tests made on various forms, is that no mammal below the monkeys and apes is capable of color discrimination.

No study of color vision in the dog has been made by means of the Yerkes-Watson method described above. So far as the writers are aware the latest investigation in this field is that of Smith (44) published in 1912. Experimentation on color-vision in dogs has been, almost without exception, of the crudest sort. Even the experimenter has not been eliminated from the situation. Prismatic colors have never been employed. Usu-

ally light reflected from colored pieces of paper, painted food containers, colored balls, and the like has been utilized. Control of the intensity factor has never been adequate and in many cases has been quite overlooked. The results reported, and they are about equally divided for and against the existence of color vision in dogs, therefore cannot be taken seriously. Perhaps the least inadequate study making use of reflected rather than transmitted light, is that of Smith. This writer has been generally quoted as having concluded in favor of color vision (see Washburn, Animal Mind, p. 156). A careful reading of his paper shows that this does not fairly represent his position and that the data he presents certainly support no such conclusion. Although Smith is inclined to suppose that certain dogs may be able to discriminate colors to a limited extent, he emphasizes his opinion that such discrimination "is highly unstable and cannot be supposed to play any part in the animal's normal existence." For all practical purposes this is equivalent to a denial of color vision. This tentative conclusion is quite in agreement with the work of the Russian school, as is indicated by the following quotation from Pavlov (35, page 132 f.): "Dr. Orbeli in a first series of experiments was unable to detect any differentiation of colours on the part of his dogs. In a second series of experiments, however, positive results were obtained in one dog, but only with great difficulty, and even in this case the experiments were still open to criticism. The results obtained by other investigators, both Russian and foreign, lead to the conclusion that colour vision in dogs, if present, is only of a very rudimentary form, and that in most dogs it cannot be detected at all."

It must be concluded, therefore, on the basis of laboratory tests that the dog's vision is decidedly inferior. The casual observations made at home and in the field do not conflict with this conclusion. In the every day life of the dog it is no doubt a supplementary sense, rather than the dominant sense as in man. In the laboratory it seems called into play only when the more dominant senses, the olfactory and the kinesthetic, fail to bring the animal success. The discrimination experiments already reported are examples, and there are others which even more clearly indicate the tendency of the animal to overlook visual clues in favor of those of other modalities. This conclusion applies only to still and not necessarily to moving objects. De Jong (24), after training his dogs to open a box by lifting a latch in order to obtain food, turned the box ninety degrees, in the dog's absence. The dogs then went to the point on the box where the latch had previously been and made the movement of the paw that had formerly served to lift the latch. This of course failed to produce the desired results, but the dog nevertheless continued to attack that same point for some time, entirely overlooking the rather prominent latch, which, although at a new place, was still clearly within his visual range. Learning to open the door with the box so turned seemed to be an entirely new problem, accomplished in the usual trial and error manner. Only after the position of the box had been shifted a number of times, and relearned as often, did the dogs finally come to respond to the latch itself, and even then not necessarily on the basis of vision alone. Experiments similar to these have been made by Johnson (20) with similar results. An even more striking demonstration of the insignificant rôle of eyesight is found in other of Johnson's experiments. He found that problem boxes were solved as readily by dogs temporarily deprived of

the use of vision as by their normal companions and, furthermore, that normal dogs worked in the dark almost as efficiently as in the daylight. Hamilton (13), Buytendijk and Hage (5), and others have attempted to facilitate the solution of problems by introducing prominent visual cues, which one would expect to be of real aid to the dogs, with but little or no effect.

Although there is little experimental evidence on the subject of moving versus still objects as visual stimuli, such as there is agrees with casual observations of a number of investigators to the effect that the dog is extremely sensitive to objects in motion. A preliminary study of the subject has been made in the laboratory of Pavlov, but no limits of discrimination have been determined.

Interesting indication of the great sensitivity of the dog to slight movements is to be found in the several examples of the Clever Hans error—an error which is as likely to occur in the study of dogs as in the case of the famous horse after which it was named. It seems probable that the cues imperceptible to us which the animal gets from the experimenter are chiefly visual, although audition may be involved here also. In the early experiments on auditory discrimination made by Kalischer (25), Rothmann (37), Swift (47 and 48), and others it seems very probable that the dogs obtained secondary cues from the experimenter, who was always present. Swift, for example, seems to give his case away in the following statement (48): "I found at first he (the dog) was inclined to react to motion rather than sound, and watched me closely for the motion accompanying the low tone, and would react to that." According to the conditions of the experiment the dog was allowed to take food from the experimenter's hand when this low tone was sounded. In spite of the above-quoted statement that the dog appeared at first to react to slight movements of the experimenter no effort seems to have been made to eliminate the experimenter in this case, and the writer goes on to assume the problem to have been learned on the basis of auditory cues. Johnson, studying the same problem (20), apparently had evidence for pitch discrimination in the earlier part of his work, during which the experimenter was present, but when the conditions were so modified that the experimenter was entirely concealed the discrimination could not be made. This indicates rather conclusively that the dog had been reacting not to sounds, but to slight movements made by the experimenter.

Olfactory capacity

The dog is popularly accredited with the possession of a remarkably efficient nose. It is through his superiority to man with respect to olfactory acuity that he has most frequently been of practical service to his master. He has been used to trail and retrieve game, to find lost articles and people, to detect fleeing and hiding fugitives from justice. Very little strictly laboratory work on the subject has been reported. None such has appeared from laboratories in this country. No doubt the chief reason for the paucity of work on olfaction, not only in dogs but in almost all animal forms, lies in the recognition by investigators of the great difficulty of controlling the stimuli in question.

An instance of the dog's olfactory acuity and, incidentally, an illustration of the difficulty of animal experimentation, is to be found in an early study of Johnson's (22). This careful investigator, while studying visual acuity in an English bull terrier, obtained such a fine degree of visual discrimination as to render him

incredulous. One by one he checked over the possible secondary criteria which might be giving the animal the clue for its choices. He was using an electric grid to punish wrong choices (in addition to a food reward), and it occurred to him that the animal might in some way be able to detect which of the two grids was electrified in a given trial. He therefore ran a control series with both grids electrified, cutting off the current on the side of correct choice only after the choice was made. The habit broke down immediately, the animal now responding quite by chance to the right or left side. It seemed that the difference in potential between the charged electrodes had caused a release of ozone, in minute quantities, but evidently sufficient to be the basis of the discriminating behavior.

The first question we should try to answer relates to the kinds of odors to which dogs will respond. Binet and Passy (2) claim that dogs respond to animal odors but not to odors arising from vegetable matter. Heitzenroeder (15) using a Spitz obtained evidence leading him to the conclusion that the threshold for odorous mixtures of animal origin was far lower in the dog than in man but that the threshold for odors of plants and perfume was lower in man than in the dog. His method was that of introducing the air carrying the odor by means of a funnel-like arrangement over the dog's nose and taking as indication of sensitivity a sniffing movement or change in the breathing rate. That lack of such overt response would indicate lack of sensitivity is to be seriously doubted. Seffrin (39) used Heitzenroeder's method and reached similar conclusions. Henning (16) recognizes three possible explanations: (1) the olfactory continuum shows prominent gaps or breaks; (2) all odors are sensed, but some types have a disproportionately high threshold; (3) such motor responses as sniffing are given, normally, only to biologically important odors. Henning apparently felt that the last possibility was most likely the true one, for in his study he used a different form of response. Henning's principal method involved the use of nine handkerchiefs scattered on the floor of an empty room. One of these was saturated with a definite odor. In an adjoining room the dog was given the opportunity of smelling the odor in question and was then sent into the test room to retrieve the scented handkerchief. The position of this handkerchief was varied from trial to trial. A Dobermann and a fox terrier are said to have retrieved without error the correct handkerchief when the following odors were used in intensities equalling the human threshold (subjectively determined): vanillin, heliotropin, cumarin, oil of rose, oil of geranium, jasmine, oil of lemon, peppermint, wintergreen, and others. A greyhound could not be trained to do this. This test gave no evidence of discriminatory ability but only of sensitivity, since only one odor was used at a time. Further tests of a rather informal nature indicated that the dogs could discriminate between food odors and flower odors.

Buytendijk (4) presents data not only on the lower threshold but on discriminatory ability. He employed two methods, principally. In the first of these, two boxes were used, exactly similar and each containing a biscuit. The lid of one was fastened shut, while that of the other could be opened. A small vessel containing a chemical, diluted in paraffin or water, stood before each box, and it was supposedly only by detecting the odors that the dog could tell which box was unlocked. Buytendijk apparently did not take care to eliminate the experimenter from the situation, and we cannot be sure

that the animal was not responding to some cue from himself. The results reported seem to indicate that the smells of nitro-benzol and benzaldehyd, which man cannot distinguish, are also confused by the dog. On the other hand, 0.01 per cent nitro-benzol was analyzed out of a mixture of 0.1 per cent each of eugenal, ionon, linalool, and zimtaldehyd. A number of other mixtures were also successfully analyzed. As to absolute thresholds, vinegar was distinguished in a dilution of $1:10^6$, salt and vinegar acids in dilutions of $1:10^5$, salt and quinine in dilutions of $1:10^4$. Buytendijk's second method made use of glass dishes which contained the odorous substances each held in a sort of basket with a handle permitting the dog to pick them up singly and retrieve them. The procedure was essentially that used by Henning with the handkerchiefs, except that but three receptacles were used at a time. Solutions of formic and of sulphuric acid containing one part in ten million were correctly responded to, as were also extremely dilute solutions of a number of other acids. All such solutions were said to be quite odorless to man. Here again there exists the possibility that the dog reacted to cues given by the experimenter.

To what practical use can the dog put his olfactory ability? In the first place it is so generally accepted that certain dogs are able to follow the trails of other animals that special tests of this ability have apparently seemed unnecessary. This does not mean, however, that a dog can distinguish between the trail of animal *x* and animal *y* of the same species nor, perhaps, that he can distinguish between the trails of individuals of closely related species, although most hunters will say that dogs readily do so. Bingham (3) reports that a setter who normally pointed birds very skillfully had on occasions followed trails which proved to have been made by turtles, and he states that other cases of this sort have been brought to his attention. It seems probable that olfactory reception is dominantly if not solely responsible for much trailing behavior. That trails are followed more readily when they have been recently made is doubtless due to the fact that the odorous particles, emanating most probably from the footprint of the trailed animal, diffuse rapidly and finally reach a degree of dilution such as to render them below the lower threshold of the dog. Tests made by Buytendijk on a German Shepherd dog (4) indicate, among other things, the effect of wind on the trail. When following a trail leading straight into the wind, or when following a trail behind an obstruction which cut off the wind the dog followed almost exactly the steps of the man being trailed. But when the trail crossed open country at right angles to the wind the dog did not follow exactly the path of the man but ran along rather uniformly from one to two meters or more to the leeward of this path.

Although Romanes' tests of the sense of smell in his female setter (36) have frequently been referred to, certain interesting details have been overlooked. It will be remembered that this animal could trail Romanes successfully even though a number of people were made to walk single file behind him in such a way as apparently to obliterate his trail. By appropriate tests Romanes found that the dog would not follow his trail when he was barefoot, in stocking feet, or wearing a pair of new boots, that the dog would follow the trail of a stranger only if that stranger wore a pair of Romanes' old boots. It was apparently the old boots which were being trailed. Romanes then proceeded to paste heavy brown paper en-

tirely over his boots, soles and all. The dog was unable to trail him when he wore his boots so covered. After walking some distance a small bit of the paper wore off the heel of one of the boots. When the dog, which had been led along the trail far behind in the meantime, reached the point where the heel had worn through and was thus making contact with the ground it picked up the trail at once and soon caught up with Romanes. This little incident hints at the extreme delicacy of the stimulus which is apparently effective in trailing behavior. A characteristic of trailing which has never been adequately explained, as Johnson has pointed out (21), is that a dog when coming upon a trail at right angles seems able to detect almost at once the direction taken by the animal or man making the trail. It seems impossible to imagine what the cue can be to such behavior.

Romanes' dog could apparently discriminate by odor his boots from other boots. A more thoroughgoing test of the ability of a dog to select objects belonging to a specific individual has recently been made by Löhner (28). In this case not trailing, but retrieving was the behavior employed to demonstrate the ability to distinguish between the odor traces left by various individuals. But one subject, a two year old female German Shepherd dog, was used, and in every case the object to be retrieved was one which had been handled by her keeper. The objects in question were small pieces of pine wood. One of these was just held in the keeper's hand, and then placed, with forceps, with ten to twenty other pieces which had not been so handled. The dog was allowed to sniff her keeper's hand and was then told to get his piece of wood. She was successful in every case. An attempt was made to discover to what extent it was necessary to handle the pieces. Apparently the shortest duration necessary to their identification was 2 seconds and the smallest surface was that touched by the finger tip. Washing the hands of the keeper in alcohol before touching the wood did not interfere with the identification. Even though four or five pieces of wood handled by others than her keeper were introduced among the dummy pieces, the dog appeared able to select her keeper's piece. At no time was the dog asked to retrieve pieces held by anyone but her keeper. Apparently these experiments were conducted extremely carefully, but, unfortunately, it is not stated whether or not the keeper, or other observers with knowledge of the correct object, were within the visual range of the dog during the selection. If this was the case (and mention would probably have been made of it were it not) the results could scarcely be accepted.

It may be, however, that a dog is capable not only of following human and animal trails but of selecting objects which belong to, or have been handled by its master. Whether this ability to identify the odor traces of an individual person extends to other than the dog's own master has not been established. Nor has it been proven that, upon being given the hat or some other article belonging to a stranger, the dog can select that stranger from among a group of persons. In spite of the fact that the dog's ability along these lines is not definitely known, evidence which depends directly upon such ability is admitted by the courts of many states of this country and also in certain foreign lands. Much more of the validity of such evidence should be known if convictions are to be made on the basis thereof. Realizing this, certain German police officials, notably Police Lieutenant K. Most, with the cooperation of Professor Pfungst conducted a series of tests a

few years ago, in Berlin. These are reported by Craig (7), who, however, fails to give the original reference. The tests were open not only to police dogs but to all comers, and retests were permitted after failures when so desired. A number of prize winning dogs of various breeds were entered and tested individually. Four types of test were given. The first involved the following of a fresh human trail among other recently made trails. No dog proved able to do this reliably, although most were able to follow a fresh trail over older trails. Among fresh trails the dogs often switched from one to another, the angles of intersection seeming to play a prominent part in determining which trail was to be followed. The tendency was for the dog to follow any fresh trail extending in the same general direction taken by the trail he had just been following, i.e. if the trail he was following in a northerly direction turned abruptly east, at a point where it intersected a second fresh trail which from that point extended northerly, the dog usually followed the second trail.

The second test involved the following of an old trail over ground entirely free from other trails. Twenty tests over trails from $5\frac{1}{2}$ to $6\frac{1}{4}$ hours old resulted in absolute failure. Trails were followed well only when not more than 30 minutes old.

The third test involved the selection from a group of objects of the one previously handled by a person who had been pointed out to the dog. In other words, this corresponds to Löhner's experiment except that other individuals than the dog's master were used. In no case did a dog make a correct choice more often than he might have by chance.

The last test was the converse of the previous one. The dog was given the glove of a person and told to select the owner, who, together with nine other men, stood in line with their backs to the dog. In no case did the men know whose glove had been given the dog to smell. This precaution prevented the "guilty" man from revealing his identity in any way. The dogs all failed in this test as completely as in the previous ones.

The conclusions drawn were that those cases of successful detection of criminals by dogs (as demonstrated by subsequent confessions) were probably made on the basis of slight movements of the criminal resulting from his fear of being detected. Those cases where a dog had apparently trailed a criminal to his lair were interpreted as examples of the Clever Hans error. It was supposed that the police sergeant holding the leash on which the dog was led while trailing often had a sagacious guess as to the probable hiding place of the criminal and, all unwittingly, led the dog to that place, rather than being led by the dog. In other words it was a case similar to the "muscle-reading" by which so-called mind-readers often successfully entertain parlor audiences. As a result of such tests, so Craig reports, the use of dogs in criminal detection is now forbidden by the Prussian government.

How are we to interpret these results? It seems to the writers that these negative results cannot be taken as definitely proving a lower degree of olfactory acuity in dogs than had previously been granted them. It is more probable, in view of the other evidence in favor of extraordinary acuity, that these tests indicate that the problems were not properly set for the dogs. To use, for the sake of simplicity, an anthropomorphic term, we have no evidence that the dogs understood what was expected of them. Negative conclusions are always difficult to support, and they are certainly not justified in the absence of evidence that the problem at

hand has been adequately set and that sufficient motivation has been brought to bear upon its solution.

We are not at all inclined to belittle the dog's olfactory acuity and feel that the bulk of the evidence shows it to be far superior to our own.

Auditory capacity

Experimental evidence on hearing in dogs appears to indicate that they are at least as sensitive as man in this respect, while their capacity for auditory discrimination is less certainly known.

Only one study of intensity discrimination has been made, that by Tihomirov, a student of Pavlov. He used an organ pipe with an arrangement for damping the sound as desired. The results seem too good to be true and are perhaps best covered by quoting from Pavlov (35, p. 135): " . . . it was found that an intensity very closely approaching the one employed as a positive conditioned stimulus could be differentiated by the dog with an absolute precision even when a pause of 17 hours was made between the two stimuli. The experimenter found himself able to detect a difference between these two intensities of the sound only when they succeeded each other immediately. . . . In the continuation of these experiments the intensity of the inhibitory tone was brought still nearer to the intensity used for the positive conditioned stimulus, and an absolute differentiation was obtained even after a pause of three hours between the stimuli. Unfortunately these experiments were conducted in our old laboratory where the effect of the inhibitory stimulus was easily disturbed, and it must be left to the future to repeat these experiments under more perfect conditions in our new laboratory."

The bulk of the experiments on pitch discrimination leave much to be desired in the way of technique. The experimenter has usually been present, and pure tones have seldom if ever been used. All investigators but Johnson have found some degree of pitch discrimination. Johnson's work was inspired by reports of some of the earlier work done in Pavlov's laboratory (by Selionyi and by Beliakov) in which it was claimed that dogs could discriminate differences of one quarter and even one eighth of a tone. Johnson justly criticizes this work in the article reporting his own results (20). He used the Yerkes-Watson discrimination apparatus employing both punishment and reward. The experimenter was eliminated. The sounds were produced by electrically driven tuning forks. To one note the dog was required to turn to the right to be rewarded, to the other he was required to turn to the left. Although the dogs were given a prolonged training series there was no evidence that they could learn to make the discrimination. Pavlov set Anrep on the problem of repeating the earlier work of Selionyi, which had not been accepted by American investigators. Anrep (1) criticizes Johnson's work on two grounds. The first criticism is methodological. It is his opinion that the problem as set by Johnson is far too complicated. The animal is rewarded for both sounds, although at different places and, similarly, when it makes a wrong choice it is punished while both sounds are being given. We are forced to agree that the Pavlov method presents the animal with a far simpler learning problem. The one note is continually reenforced by food, the other note is never so reenforced.

Anrep's second criticism relates to the production of the tones, it being his claim that it is impossible to eliminate entirely the noise of the "make and break" when using electrically driven

tuning forks. Anrep used electric resonances and a synchronous motor, driven by alternating current producing, supposedly, a sinusoidal curve. As a sound generator in the experimental room a pair of telephones was used. These were placed close together, each attuned to the pitch which it was to transmit. Anrep reports discrimination in the case of one dog of two notes differing but slightly in pitch, the one 637.5 d.v. and the other 680. d.v.

The controversy regarding pitch discrimination in the dog can only be settled by further work.

The only data on the upper limit of the auditory range in the dog come from the Leningrad laboratory (Bourmakin, Andréev). These indicate a sensitivity to sounds far above the highest note audible to man, or up to 100,000 d.v. Other work by Pavlov's students indicates remarkable discriminatory ability for notes alike in pitch but differing in timbre or tone color, and also extreme sensitivity to differences in the periodicity of the beating of a metronome.

That the dog is able to localize the source of sounds with reasonable accuracy has been demonstrated by Johnson (20) although he did not study the limits of their sensitivity in this respect.

Regarding the ability of the dog to respond to the human voice there is a wealth of anecdote but a paucity of experimentation. There is, of course, no question but that they can hear spoken words, but as to the number of spoken words that can be discriminated by a given trained dog there is very little evidence. It has been proven in the case of certain dogs who have been supposed to give differential response to a large number of words that they were merely following a routine, that if the commands were given in an altered order the dog would respond as though the original order had been repeated. Don, the talking dog, is the classic example of response to routine (19). A bull terrier, Jasper by name, was claimed by its owner to have an understanding of several hundred words. No thoroughgoing tests were made of the dog, but Watson was inclined, as a result of observations of his behavior, to consider such a claim far too extravagant. (55, page 315).

Edinger (9) trained a female Shepherd dog to respond appropriately to a number of simple commands. She could turn the knob of a door and open it. She could also close doors but often confused the two responses, turning the knob of an open door, and so on. If she was told to close a door which was swung open *away* from her she was quite helpless, not making the response obvious to us of going around behind the door and pushing it shut. Edinger believes that the responses were not given to the spoken commands as words, since nonsense words served just as well if corresponding inflections were maintained. Schiche (40), on the other hand, believes dogs to be capable of a rather fine degree of discrimination of consonants. He trained police dogs to sit at the command of "Setz" and to lie down at the command, "Platz." To such similarly sounding syllables as "seck," "retz," "petz," and "ketz" the dogs did not react. We judge, however, that the experimenter was always present.

Perhaps the dog for whom the most astounding performances have been claimed is the Airedale, Rolf, often referred to as the dog of Mannheim (27, 30). This dog was usually present during the daily lessons of some young children. One day while chastizing the children for failing on some simple arithmetical problem the tutor remarked that the problem was so simple that even Rolf

could solve it. Thereupon Rolf proved himself worthy of such opinion by tapping out the proper answer with his paw. This led to a systematic education of the dog involving not merely the simpler arithmetical problems but also square roots and so on. The dog also learned to spell, using taps of the paw to represent letters. It is said that at the suggestion of his mistress he manufactured his own alphabetical system, and it is claimed by his proud owners that, apparently in the interests of efficiency, this system involved the fewest number of taps for those letters which are ordinarily used most frequently. It is difficult to evaluate the so-called tests made of this dog because of their uncritical nature. Every opportunity was given for the operation of the Clever Hans error. Only one incident reported cannot readily be explained on that basis. In this case the cards, on which the problem given the dog was presented, were shuffled by the observers and shown the dog at random and without any of the observers knowing just which card had been presented, and thus what reply to expect. Unfortunately these conditions were not maintained often enough to yield results of statistical validity. The attention of Claparède, one of the scientists to test the horses of Elberfeld, was called to the dog, and he planned to subject him to critical tests. Probably the most brilliant thing Rolf ever did was to be taken suddenly ill soon after Professor Claparède's arrival.

Other modalities

Of the other sensory modalities little can be said, since there are at present no data upon which we might base an estimate of sensitivity and threshold values. That kinesthetic stimulation is highly important has already been suggested in connection with our consideration of the rôle of vision. It apparently dominates visual stimulation in determining the behavior of the dog under ordinary conditions. Beyond the fact that dog and man are sensitive to the same general types of tactual, thermal, gustatory, and electric stimuli little is known. To summarize: it seems probable that the average dog is far more sensitive to odors than is man; that he is not strikingly unlike man with respect to sensitivity to sounds; that his vision for still objects is decidedly inferior to that of man, while his acuity with respect to moving objects is great, although there is not sufficient data to warrant a comparison with man in this respect.

Learning ability

The learning ability of dogs has been tested by means of the usual laboratory methods. Dogs have been used by Thorndike (53), Johnson (20), and others on the problem box, by Szymanski (49) in the maze, by Hamilton (14) in a quadruple choice device, by Hunter (18) and by Walton (54) on the delayed reaction set-up and by Shepherd (41) in situations involving the pulling of a string to draw food into their reach. Apparently they have yet to be tested by the Yerkes multiple choice method. One gets a clearer impression of the dog's learning ability not by perusal of the quantitative results but by a comparison of these results with those obtained on other animals.

Without going into detail it may be said that as tested on such devices the dog appears to be superior to the cat, slightly inferior, perhaps, to the raccoon, and probably inferior to monkeys and apes. This last conclusion is, however, based only upon tests which are much more suited to the motor equipment of the monkeys and apes. Even though a dog and a monkey might be equal in intelli-

gence we should expect the latter to be more adept in the manipulation of knobs, sticks, strings, and the like, because of his well developed hand. Perhaps if monkeys and dogs were tested on a similar maze, where the responses involve only locomotion, the standing of the two forms would be reversed. We have no way of knowing, however, for this has not been done. Similarly, the only demonstration of the raccoon's superiority to the dog has been on a problem box involving manual manipulation. The raccoon's forepaw is modified so as to be fairly efficient in grasping articles. The dog's paw is, of course, ill suited for such uses and, as a matter of fact, a dog often prefers to use his mouth. Dogs have shown very little ability to imitate each other or man, but this lack does not place them below other animals, since experimentation has shown that true imitation is rarely found in any animal form, even among the higher apes.

A few words on the dog as a psychological subject may not be out of place. As is well known the rodents are represented in behavior studies by the white rat. The selection of a single representative species upon which all experimenters interested in the lower mammals should do systematic work is, of course, a great advantage, since it renders possible the collation and comparison of a vast amount of data. If some workers used squirrels, others guinea-pigs, others weasels and so on, this valuable intercomparison would scarcely be possible. Among the Carnivora there has not been such a definite concentration upon a single form, although the dog has been the chief object of study. There are a number of reasons why the dog would seem to be the logical animal to represent this group. In the first place more is already known of his sensory and learning capacities than of those of the cat, the raccoon, the porcupine, or any of the other animals of this group which have been subjected to experimentation. In the second place less interference by emotional disturbance is encountered in the case of the dog than in animals not so able to adapt themselves to the necessary experimental situation. That the emotional status of the animal during testing is highly important and should be kept as constant as possible does not seem to be sufficiently recognized. This is especially true of the higher, more complex forms. We cannot blame pioneers for having tested animals under conditions rendering them more or less frantic with hunger and fear. But it seems surprising that such a recent worker as Williams (56) should take seriously his negative results on form discrimination in dogs when his subjects were, judging from his descriptions, highly nervous and fearful during the tests. To quote: " . . . . a dog occasionally develops the obsession that he can not get out of the blind alley and stands yelping, enduring for a time the punishment (electric shock). In such a situation it may be necessary to move up the secondary coil thus making the electric current stronger till it is of sufficient intensity to overcome the obsession and force the dog to become more diligent in search of a way out." Williams used punishment only. To quote again: "With the method of punishment by electric shocks, little time need be wasted, if all parts of the apparatus are in good working order, as the animal can be forced by the shocks to move to any part of the apparatus at the will of the operator." No doubt such an investigator would consider it a waste of time to become sufficiently *en rapport* with the dog to permit the use of the normally strong desire of a dog to please his master as motivation.

This brings us to the third qualification of the dog which renders it capable of becoming an ideal laboratory subject. The dog is unquestionably more sensitive to the whims of a man who has won his confidence than is any other carnivore, or perhaps any other infra-human animal, for that matter. The cat, for example, is scarcely at all dominated by man, except in his rôle as provider. Thus starving or using some such punishment as electric shock is practically necessary to produce sufficient motivation to insure their attacking laboratory problems. Even in monkeys and apes the problem of motivation is a difficult one if we may judge from reports in the literature. The dog has continually demonstrated his ability to adapt himself readily to the wide variety of conditions which man has imposed upon him. He has cooperated with man in war and in peace, in the forests, in pastures, and in the city. Nor has he failed to cooperate even in the psychological laboratory except when no effort has been made to deal with him in a manner befitting his high degree of complexity and sensitivity. Many examples might be given to show his willingness to play his part in experimental situations in the absence of harsh forms of motivation. The dogs used in the Leningrad laboratory are said to jump up onto the experimental tables without command and to lift up their feet one at a time to permit the adjustment of the necessary harness. An early study of Hamilton's on a young bull terrier (14) gives an admirable instance of adjustment to an experimental situation. The problem presented to the dog was an extremely difficult one, that of releasing himself from a box by the manipulation of a system of pedals. This dog worked daily on the problem over a period of many weeks with, apparently, unflagging zeal even though no punishment was used and the reward consisted not of food but only of petting and a few kind words. It seems only reasonable to suppose that an animal working under natural and undisturbing conditions would be more nearly capable of giving a performance record, whether of discrimination or of learning, that would represent its maximum capacity than would an animal working under the stress of punishment or too severe hunger. The dog is one of the few animals which will work without such motivation.

One of the reasons for the discrepancies that exist among experimenters on the dog's capacities is no doubt the fact that all sizes and sorts of dogs have been used from highly bred bull terriers to an assortment of mongrels. It would no doubt be well to settle upon a representative breed for systematic experimentation, but the writers are at present in no position to make a definite proposal as to which of the many breeds is best suited to the purpose.

II. RECENT TESTS OF THE ABILITY OF "FELLOW" TO RESPOND TO VERBAL STIMULI (OR TO UNDERSTAND HUMAN LANGUAGE)

Fellow is a thoroughbred German Shepherd male, between 4 and 5 years of age, with a long line of famous blooded ancestry behind him, and owned by Mr. Jacob Herbert of Detroit, Michigan. Mr. Herbert has made a hobby of fine dogs for years and selected Fellow from among scores that he has bred, and sought to teach him in various ways to understand human language in the sense of responding in the appropriate manner to commands. This type of training is, of course, not especially new. The verbal cue has been often employed in professionally trained animals, and everyone has taught his dog to do, upon proper command, a few tricks at least. But Fellow, as Mr. Herbert

explains, has been talked to constantly almost from birth in much the same manner as a young child during the years of taking on language, and it was this fact of the extensiveness of such experience and its possible effect upon the dog that made his case particularly interesting. Mr. Herbert believes that Fellow has picked up from this long contact with mankind some four hundred or more words, and that he understands these words in much the same manner as a child under the same circumstances would. By the term "understanding" Mr. Herbert seems to mean no more than that definite associations have been formed between specific words on the one hand and specific objects, places or acts on the other. As a layman he has no opinion to offer regarding any so-called mental or subjective content of the dog's mind in connection with these words, claiming only that the words operate in some manner as the essential signals in determining the dog's behavior. From conversation with him we gather that he doubts the ability of the dog to recall the words voluntarily, in a manner supposedly characteristic of human thought processes, and thinks of the dog as being capable of merely recognizing or identifying the object, place, or act when the word is spoken in the presence of the corresponding thing or event. He does not consider the facts in the case to offer any positive evidence of reasoning in the more technical sense.

Our personal acquaintance with both the dog and his owner began on September 29 last when we went to the Pasadena Hotel, New York City, at the request of Mr. Herbert to witness the performance of Fellow and to make such tests as we might see fit. Mr. Herbert was anxious to have his opinion of the dog's ability checked up by psychologists.

Aside from the matter of responding to words, no special claims were made for the dog. As his master explained, Fellow was not a trick dog—had not been trained to perform any unusual stunts. He had quite successfully played, indeed, the usual rôles allotted to his species in movie-melodrama—those of protecting the helpless and saving the drowning child, had starred in "Chief of the Pack" and other animal cinemas, but no special effort had been made to develop in him unusual motor performance. His claim to special attention lay in his accomplishment of responding to a large number of human words in some sense or other, and the problem before us was to determine in precisely what sense.

Mr. Herbert recognized the possibility of error in a layman's opinion regarding the ability of Fellow along linguistic lines and received us in a questioning rather than an argumentative mood. From the first he showed every willingness to cooperate with us in an honest effort to discover the facts in the case. In truth, Mr. Herbert deserves great credit for the straightforward attitude which he has maintained throughout the tests, regardless of their effect on his own personal opinions concerning the ability of his companion and friend. He has not sought to explain away failure in certain cases by insisting that the tests were unfair, the dog indisposed or tired, or by any of the escape mechanisms often employed by professional trainers to preserve the reputation of their protegé, or their own personal illusions of special or mysterious genius. That the owner of the dog was thus able to enter into the scientific spirit of the enterprise and give us a free rein in testing the dog had much to do with whatever success has attended our efforts.

Our first examination of Fellow was strictly private, only one person being

present in addition to Mr. Herbert and the writers. We watched the dog perform for half an hour or so—remarkably well it seemed to us in spite of our chronic skeptical attitude. We noted that no attempt was made by the owner to use identical phrases in the commands covering the same preformance, nor was any set order followed in the performances. The commands were given in a natural conversational tone as if the owner were holding a conversation with the dog. We were quite convinced before the examination was over that the performance of the dog was far above the level of routine so characteristic of the usual animal trained for purposes of exhibition. Even when we, ourselves, determined the order of the commands in a hit and miss manner the performance was perfect. Our opinion that the different acts were quite isolated from one another and involved no element of routine whatsoever has been fully borne out by all later tests.

The problem as to the nature of the stimulus cues determining the responses of the dog could not, of course, be so easily disposed of. The first point to settle was whether the essential stimuli were actually auditory or not. For after all the dog might be depending upon unintentional gesture, or other visual cue so long as he performed always in the presence of his master. The possibility of the "Clever Hans" error must be effectually ruled out in view of the fact that Johnson (20) had found it to be a complicating factor in his work on auditory sensitivity in dogs. Certain pitch discrimination habits, or what seemed to be such, broke down entirely when the experimenter absented himself from the room during the experiment.

In the absence of a screen, Mr. Herbert was stationed in the bathroom of the suite and gave his commands through the closed door while the writers remained in the room with the dog to observe and to give the necessary signals for the successive commands. We were very careful not to aid Fellow in any way by movements of body, head or eye. Although not perfect, the dog's performance was on the whole quite satisfactory, and especially so in view of the fact that the arrangement of having the master absent was entirely new, and the commands were noticeably less audible. It was evident that visual cues from Mr. Herbert were quite unnecessary to successful response in many cases at least, the essential stimuli being auditory in character.

It would have been desirable to run a series of control tests to determine more precisely the nature of the auditory cues and particularly what, if any, language elements were involved. We were handicapped at this point, however, by the fact that Fellow is a one-man dog and has been trained not to respond to the commands of others than his master. Such training is perhaps necessary if an animal is to play his part well on the stage or in a cinema rôle. It was impossible to carry out our original intention, therefore, of making systematic tests in which the commands should be given by other persons with varying pitch and different intonation. We had thought of introducing a woman's voice in this connection. We did find that Fellow would obey the commands of persons with whom he has been associated for some time, after getting a nod of approval from his master. Furthermore, Mr. Herbert varied his own voice in pitch, intensity and intonation—sometimes giving the commands in a monotone—without disturbing the dog's performance.

It was evident that the dog has associated certain sounds, of the human, verbal pattern type, with definite responses, but

was this equivalent to understanding words in the human sense? The question as to whether a spoken word is a true language element, or merely an auditory stimulation of the non-language type, is after all a highly technical one, and depends in the last analysis upon an acceptable definition of an elementary language element. So far as the present writers know a satisfactory distinction on this point has not as yet been made. If we define too strictly, many responses of the human that we ordinarily think of as language are probably not really such, whereas a broader definition of the term might easily overthrow the distinction entirely. Perhaps we are here faced with the usual difficulty of scientific classification, where genuinely discrete elements are not involved but only differences in degree. May it not be that here as in most cases we have not distinct classes of stimuli—language vs. non-language—but a graded series of stimulus situations in which the application of arbitrary classificatory criteria is almost worthless, if not absolutely misleading? The problem is not strictly confined, moreover, to studies of auditory responses in infra-human forms. In the human infant and young child it bobs up again and again to disturb the human psychologist. A genetic account of the development of language in the child would undoubtedly throw much light on our own problem. Perhaps it would be found that in this case words are responded to at first as purely auditory stimuli, and as development proceeds these sounds take on more and more of the attributes which we have come to associate in our thinking with language in the more exact sense.

As a result of the completion of this first examination of the dog we issued the following statement to the press in order to avoid the usual scandal of newspaper accounts. That we were not able wholly to escape will be seen when this statement is compared with the headlines that have appeared both at home and abroad in connection with the test.

> We have just completed a test of an hour and a half on "Fellow," the famous movie-actor dog and it is a most remarkable dog in many respects. It is certain that the dog obeys commands given by the human voice with remarkable speed and facility. The commands do not need to be given in any set order as the dog has been taught so well that a routine line of command and performance is not at all necessary. This is the more surprising in view of the fact that no punishment has been used in training the animal—he has been given much the same treatment by Mr. Herbert as one would give a child.
>
> One point is definitely settled—the dog does not require gesture in addition to the human voice, at least in many of its performances. Mr. Herbert gave commands from an adjoining room with the door closed, and with no one but total strangers in the room with the dog. The animal would go to the window, go into another room and do various things, pick out objects from among several, etc., when the commands were given from the room in which Mr. Herbert was concealed.
>
> One point remains to be settled, if indeed it can be settled at the present state of our knowledge of animal behavior. That is, does the dog understand words in the human sense? This is a difficult point to settle inasmuch as it is possible for an animal to obey commands to words, not as words but as sounds. Such tests as were made, that of changing the tone in which the commands were given and of giving confusion commands still leave the matter in doubt. Personally we are of the opinion that the dog has learned to associate certain sounds, rather than words in the human sense, with the proper objects and commands. However, the large number of associations clearly mark the dog as most extraordinary.
>
> (Signed) Professor C. J. Warden and
> Dr. L. H. Warner.

It will be noted that the statement is in general conservative and contains no comparison whatsoever between the intelligence of Fellow and that of a child. Such comparisons are manifestly absurd since a common rating scale, or test applicable to both has not yet been de-

vised, if indeed it ever can be. The newspaper headliner to the effect that we had found the dog equal in intelligence to a child of six or eight years of age must have been invented by the printer's devil. Or perhaps it originated from a dullard's confusion in connection with a statement once made by Mr. Herbert that the dog understood as many words as a child of this age. The newspaper publicity began when Mr. Herbert came out to Columbia, at our request, to make a demonstration performance (not a test) before a class of graduate students in comparative psychology. The press got wind of this demonstration and attended in a body, and the next day five of the principal producers of movie news reels were on hand with their usual irresistible insistence.

Although Mr. Herbert and Fellow were very busy a short series of tests to be carried out in the psychological laboratory at Columbia was arranged. It seemed desirable to repeat the test designed to rule out the possibility of visual cues, under better controlled conditions (that is, with no one at all present during performance) and to secure data regarding the total number of words to which the dog would thus respond. Furthermore, we wished to test the ability of the dog to identify and retrieve a given object from among several upon command. The usual stage performance of Fellow is from 20 to 30 minutes whereas our test periods ranged from one to two hours, since we wished to secure as much data as possible at such times as the dog could be placed at our disposal. The use of long test periods was unfortunate inasmuch as Fellow often gave every indication of being weary of his task before the end of the longer periods, although continuing to work when duly encouraged by his master. Aside from the word "Shame" or "That's no good," spoken in a somewhat scolding tone, no punishment has ever been used either in training or testing the dog.

In re-testing the dog's ability to respond to commands in the laboratory Mr. Herbert and both experimenters were concealed behind screens so that there was no opportunity whatsoever for the Clever Hans error to enter into the results. Several chairs, tables, and such other objects as were to be used, were placed in chance locations about the room, which included also two windows and one door. The behavior of the dog was observed through a slit in the screen by one observer and recorded, while the other reported to Mr. Herbert and indicated the command to be given next. Reaction times were not taken in this series of tests. On all three days the command-performance test was given after Fellow had been working for an hour or more at the retrieving-objects test, to be described later, and naturally he was not at his best on all occasions.

It soon became apparent that certain commands could be carried out as perfectly under our test conditions as when the master was present but that others could not. After some attempt at analysis we discovered that the repertory of commands classified readily into two quite distinct groups. Type I, as listed in table 1, did not involve any very definite identification of object or place, but consisted of some movement of the animal's body in whatever place he happened to be at the moment. Type II, on the other hand, required the animal to identify and orient himself toward some object or place after the command had been given. The former response could be made immediately after the command issued, the latter usually involved a delay of considerable length. In fact, it constituted a typical delayed reaction situation except for the fact that the signal was a sound, or word instead of a light and presupposed that a

TABLE 1

Items selected from this list in command-performance test

TYPE 1—NO SPECIAL ORIENTATION TO OBJECT OR POSITION REQUIRED

1. Sit (on haunches)
2. Sit down (on all fours)
3. Stand up (when sitting or lying down)
4. Stand still
5. Stand up high (against some near object, as wall etc.)
6. Step back
7. Step up closer (to object or person)
8. Roll over
9. The other way (rolls back again)
10. Turn around
11. Jump up, or get up (when sitting or lying down)
12. Jump up high (against near object or person)
13. Lay down (on haunches)
14. Lay down all the way (prostrate)
15. Lie still (when down)
16. Lay (or put) your head down (lays head down to one side)
17. On the other side (moves prostrate head to other side)
18. Turn your head
19. The other way (turns head back again)
20. Lay (or put) your head on the chair (or other object in front of him)
21. Lay (or put) your head on the lady's (or gentleman's) lap
22. Put your foot on the chair (in front of him)
23. The other foot (puts other foot on chair)
24. No, the other chair (or object or person near by)
25. Close your mouth
26. Look up high
27. Look up high at the squirrel (from watching squirrels in trees)
28. Listen to me (cocks head sidewise and looks intently at Herbert)
29. Bring the dollar (or other object in mouth or near by) to me
30. Go and take a walk (walks about slowly)
31. Go and take a run (runs to convenient spot and micturates)
32. Go and take a walk around the room
33. Go into the water (to swim)
34. Go over to the lady (or gentleman near by)
35. Stand up close to the lady (or gentleman approached)
36. Put your head up close to the lady (or gentleman approached)
37. Can anyone hurt Herbert (or other person pointed out) (barks loudly)
38. I don't trust him (barks and attacks)
39. He (she or they) is all right (ceases barking and attack)
40. Keep your eye on him (or them) (barks and attacks)
41. Careful! (ceases barking and attack)
42. Take care of him (her or them) (assumes protecting attitude)
43. Let no one touch him (her or them) (Even master cannot touch person)
44. He is a newsboy (barks and attacks)
45. There is a newsboy outside (goes to door and barks loudly)
46. Stay here, I'll be back (when leaving the apartment)
47. Speak or talk (low guttural growl)
48. Go outside and wait for me (dog leaves room and waits outside)
49. Jump up in the front (or back) seat (from other seat in car)
50. Go along with the lady (or gentleman)
51. Still (wait, stop, quit that, never mind) (stops whatever he is doing)

TABLE 1—*Continued*

52. That is all (or you can run and play now) (signal to quit work)
53. Do that once more (repeats act just done)

TYPE II—SPECIFIC ORIENTATION TO OBJECT OR POSITION REQUIRED

1. I have lost my gloves (or other object) (searches and finds object)
2. Go and get my gloves (or other object in room)
3. Go in the other room and get my gloves (or other object)
4. Go and find my keys
5. Come over to Herbert
6. Come and let me take your collar off (goes and holds out head)
7. Go and find professor (or other acquaintance)
8. Go and look out of the window
9. Now go to the other window
10. Go and put your head on the chair (table, or other object)
11. Go and jump up on the table (chair, or other appropriate object)
12. Go to the front (or back) door
13. Go and put the dollar (or other object in mouth) on the table
14. Go and find the cook
15. Come over to me and let me brush you (goes and takes proper attitude)

word-object association had previously been formed sufficiently strong to carry over the interval and lead to a recognition of the object when the latter came finally within the field of vision. The work of Hunter (18) Walton (54) and others on the delayed reaction experiment, which is relatively simple compared to the present test, should have served as a warning against expecting favorable results in this case. We know of no instance in which even the higher apes have actually demonstrated their ability to pass such a test when all visual cues have been ruled out; and of course Fellow could perform even the type II commands when his master was not behind the screen.

Without further tests we are unwilling to say that the dog cannot come up to the type II level of response, since the arrangement of hiding the master behind the screen was new and perhaps disturbing to Fellow. This may have been due, not altogether to lack of visual cues, but perhaps also to the fact that the dog was, under this condition, removed from his usual position for performing, i.e., on the stage in front of his master. Some evidence for disturbance arising from this and other conditions imposed by the test can be gathered from a close study of the detailed records.

October 30, 2:00 P.M. (all three persons present behind screens). The following commands (type II) were given along with many of the simpler sort (type I), all of the latter being correct:

1. "Jump upon the table"—Correct.
2. "Put your head on the chair"—dog jumps up on table again.
3. Command repeated twice—dog hesitates, looks toward screen, goes over to the window and looks out.
4. "Go over to the door"—dog leaves window and stands near screen.
5. "Go look out of the window"—dog jumps up on table near by.
6. "Put your head on the table"—dog looks at and approaches screen.

It was now decided to make a deliberate attempt to confuse the dog, by having Mr. Herbert come from behind the screen and issue the commands, at the same time looking away from the place or object

which the dog was supposed to approach in performing, with the following result:

1. "Go put your head on the chair"—dog jumps up on table at which Herbert is looking.
2. "Jump over the chair, good dog"—dog goes over to window at which Herbert is looking.
3. "Go over to the door"—approaches table at which Herbert is looking.
4. "Go over to the door now, I say"—goes to window slowly, toward which Herbert has turned.
5. "Go take a walk around the room"—dog goes to door at which Herbert is looking.

Mr. Herbert was then blindfolded and the test repeated to see whether Fellow got his cue from watching his master's eyes or from the general orientation of head and body. Similar results were now obtained showing that the latter factor is most likely the important one.

The dog was again tested as before with all persons present behind screens, and with similar results on November 4, and November 10. Only two commands of this order out of a total of 20 were properly executed—less indeed than pure chance should give. On their face these results seem to show that Fellow does, and must use visual cues in carrying out commands of this type. It should be pointed out, however, that not all items of the type II were tried out under test conditions and some of them would appear to be much easier than others. This point did not occur to us until we were analyzing the data a few days ago, and it was then too late to make further tests. The fact that the dog did not fail at all on the more than fifty different commands of type I, even when these were given over and over again along with the more difficult sort, shows very clearly the ability of the dog to form associations between sounds, or verbal patterns, and definite acts on his part. Furthermore, it will be seen that the dog did very well indeed on the retrieving-objects test, which happens to be the third item in our type II list, but which was tested under a more natural arrangement. We have the feeling that if Mr. Herbert would use the screen arrangement for a while in training the dog until he became accustomed to performing with his master out of sight, many if not all of the commands of type II could be carried out successfully without any visual aids whatsoever. Even in the present results, it is only the *object*, or *place* in connection with which the act is to be performed, and not the act itself that seemed to require visual cues. It is more than likely that a greater amount of practice had been given the name-act associations than the name-object, or name-place connections and hence we should expect the former to be more firmly fixed and more easily utilized.

The retrieving-objects test

According to Mr. Herbert, a large number of common objects and places are known to Fellow by name. The partial list which he gave us included the following items:

table, chair, pillow, bed, sofa, window, door, back door, front door, car, truck, elevator, water, milk, tree, wall, keys, brush, lady, gentleman, baby, boy, little boy, big boy, girl, little girl, big girl, dog, cat, puppy, shoes, baby's shoes, baby's doll, gloves, package, hat, coat, dollar (silver), money (paper), stick, ball, roof, fence, house, horse, post, lap (of person), collar, strap (leash), bite (of food), foot, head, mouth, paw, names of some 40 people and other dogs in Detroit, etc. In addition he supposedly recognizes certain terms of praise (good dog, that's fine, that's right) and certain words indicating blame (shame, that's no good).

The retrieving-objects test was designed to determine to what extent genuine name-object associations had been formed as he assumed. A number of familiar objects were placed in a room in one corner of

which an observer with stop watch was seated behind a screen. Mr. Herbert was stationed along the wall outside the room about six feet to the right of the open doorway and hence completely out of view of the objects located some 15 feet inside the room on a line with the door. The objects when retrieved were returned before the next command by a third person stationed outside the room with Mr. Herbert, who distracted the dog in the meantime by playing with him. The dog always stood outside the room facing his master when the commands were given. He must then turn about, go to the door, enter it and approach the objects lying 15 feet ahead and retrieve the proper object. The commands were often repeated but great care was taken not to repeat a command after the dog had reached the threshold of the door. This means, of course, that we have here, as in the case of all type II situations, a delayed reaction experiment and not a simple discrimination or object-recognition set-up. Inasmuch as Fellow moves about rather deliberately the interval of delay between the auditory signal (command) and the essential response (picking up the proper object) was quite considerable. The delay was never less than 5 nor more than 35 seconds and in most cases was about 15 or 20 seconds, as can be seen from table 2.

A preliminary test, October 30, in which at first ten and later five objects were employed, led to the decision to use only three objects in the test proper. A large number of objects could not be placed in the room so as to be equally accessible to the dog on approaching them, and the objects themselves naturally differed greatly in size. The low visual acuity of the dog for still objects has already been commented upon and suggests the need of ruling out any large differences in discriminability of objects in making tests of this sort. Three of the following five objects were used in each test: a man's kid glove, a seven inch scrub brush, a hotel key with tag attached, Fellow's chain collar, and a package 4 x 5 x 1 in. in size. The three objects were placed in a row about 2 feet apart and the order kept constant during each of the three test periods.

The results of this series of tests (table 2) are rather encouraging in view of the difficulty of the task. According to chance 12 of the 36 responses should be successes and 24 should be failures. Only 15 definite failures occurred as compared with 16 clear cut successes. Three of the five doubtful cases should probably be counted correct since the proper object was actually retrieved after a wrong object had first been picked up and dropped. The other two doubtful cases occurred in connection with the return by the dog of the wrong object brought on the previous trial. He failed to drop the returned object and came back with both it and the correct one in his mouth. These should probably be scored errors. On this accounting 53 per cent of the responses were correct as against an indication of $33\frac{1}{3}$ per cent by chance. The general arrangement of this test was more natural than the earlier one in which Mr. Herbert was concealed behind the screen, since the dog now came in contact with his master between trials. Fellow showed a slight tendency to bring the same object that he had brought the previous time, but this does not account for many of the errors. A more important factor was probably the relative ease with which the various objects could be picked up. Fellow has lost two teeth on one side, which interferes somewhat with the use of his mouth in retrieving objects. He appeared to avoid the package when it was lying down flat, and therefore difficult to pick up,

TABLE 2

Retrieving-object test

NUMBER OF TEST	OBJECT	COMMAND REPEATED	RESPONSE*	DELAY IN SECONDS	SCORE
			November 4, 10:45 p.m. (key with tag, collar, brush)		
1	Collar	2	n-brush, p-collar, d-collar, n-key, r-collar	20	S
2	Key	2	p-key, d-key, r-collar	20	F
3	Key	2	ret-collar, d-collar, r-key	15	S
4	Brush	0	r-collar	20	F
5	Brush	2	ret-collar, r-brush	30	S
6	Collar	2	r-collar	10	S
7	Key	4	r-collar	10	F
8	Brush	2	n-package, r-brush	15	S
9	Key	2	r-key	20	S
10	Package	4	n-brush, r-key	20	F
11	Brush	4	p-key	17	F
12	Brush	0	ret-key, r-brush	18	S
			November 8, 8:45 a.m. (glove, package, brush)		
1	Glove	2	r-glove promptly	10	S
2	Package	3	p-glove, looks out window, turns and d-glove, r-package	16	?
3	Brush	4	goes to window and looks out, turns, r-brush	15	S
4	Package	2	p-glove, d-glove, r-package	15	?
5	Brush	2	approaches slowly and r-package	15	F
6	Glove	2	p-glove, d-glove, r-package	25	F
7	Brush	4	p-glove, goes to window, returns to objects, r-glove and brush (window appeared to be distracting dog, so shade was drawn)	35	?
8	Glove	2	p-glove, d-glove, r-package	20	F
9	Glove	2	ret-with package, p-glove, r-package and glove	30	?
10	Brush	0	r-brush promptly	10	S
11	Package	5	r-package promptly	20	S
12	Brush	2	r-brush promptly	15	S
			November 10, 10:30 p.m. (package, brush, glove)		
1	Glove	3	moves slowly, r-glove	30	S
2	Brush	1	n-objects in order, r-glove	10	F
3	Glove	1	r-brush	15	F
4	Package	1	r-brush	15	F
5	Glove	1	r-glove	5	S
6	Brush	0	p-package, walks toward window, r-package	20	F
7	Brush	1	p-glove, d-glove, r-brush	20	?
8	Package	0	r-package	10	S
9	Brush	2	r-package	10	F
10	Brush	1	ret-package, d-package, r-brush	30	S
11	Glove	1	r-package	15	F
12	Glove	0	ret-package, appears tired, looks out window	30	F

Total number of responses..... 36
Failures..... 15
Successes (certain)..... 16
Successes (doubtful)..... 5

* n = noses; p = picks up; d = drops; r = retrieves; ret = returns.

although not when it was placed up on edge. The brush was also avoided when the stiff fibres were upturned and likely to irritate his nose, but was picked up readily enough when turned the opposite way. Strict control of this factor was not possible at the time, otherwise we feel the results of the test would have been more satisfactory.

The results here presented need to be greatly supplemented and the testing of Fellow extended in several directions before a true evaluation of the dog's ability can be arrived at. However, there would seem to be no doubt that scores of associations between verbal stimuli and definite responses have been well fixated by the patient teaching of Mr. Herbert during the past several years. The evidence for associations between verbal stimuli and objects or places would doubtless be forthcoming if a test were arranged in which object-discrimination could be made without the element of delay between stimulus and response entering in. We hesitate to make an interpretation of the present findings in terms of the dog's capacity for making a delayed reaction, on account of the meagreness and inconclusiveness of the data. In the type II command, which really includes the retrieving-objects test, we have a delayed reaction in which the essential signal for response is an auditory associate of the object, or locality in space, in connection with which the response must occur. Since the auditory stimulus gives no clue as to the localization of the object or place, orientation cannot be had as in the usual delayed reaction situation by the maintenance of gross bodily attitudes. If further tests should reveal certain evidence of such ability, as is more than suggested by the results here reported, then the dog would merit a much higher rank in the scale of mental evolution than most of us have been willing to accord him in the past.

This paper was read by the senior author before the Galton Society, Museum of Natural History, New York City, in connection with a demonstration of Fellow by Mr. Herbert before the Society on Friday, December 2, 1927.

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THE HISTORY OF WHALES—THEIR ADAPTATION TO LIFE IN THE WATER

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CETACEANS are air-breathing warm-blooded mammals, generally having pointed heads, torpedo-shaped bodies, fin-like fore limbs, and horizontal caudal flukes. All external structures and protruding organs which might offer resistance to the water have been either eliminated or sunk below the surface level. This group embraces the extinct zeuglodonts (Archaeoceti), the whalebone whales (Mysticeti), and the toothed whales (Odontoceti), including porpoises, dolphins, beaked whales, and sperm whales.

Naturalists and sea-faring people have been recording their observations on whales for many centuries and, although early literature dealing with the group contains much that is fanciful and little that is real, it is evident that whales and porpoises have long been objects of interest to mankind. The existing cetaceans are so well adapted for a continuous life in the water that naturalists of the Middle Ages believed that they must belong to the fish tribe. John Ray (1671) was one of the first to discover that the relationships of the cetaceans were with land mammals rather than with the fishes. Subsequently these animals attracted the interest of other naturalists, many of whom published their observations, so that the literature relating to cetaceans now comprises several thousand titles. Study of the anatomy of living whales and the bones of extinct species has led to many interesting speculations.

Why the progenitors of the whales forsook the land is a tempting field for speculation, but while we do know that some archaic land mammals were induced to take to water, the reasons for this action do not admit of direct proof. It is possible that the forebears of the whales may have thus found either a safe refuge from more active predatory types, or an abundance of food in shallow water and along the shores, and available data indicate that the late Sir William Flower (1883) was not far wrong when he suggested that the ancestors of whales frequented fresh water and that search for their remains should be made in the fresh water deposits of the Cretaceous period. Many anatomical and physiological adjustments were necessitated as these mammals became better adapted to their aquatic surroundings, and those which became perfectly adapted to this sort of habitat had to undergo a number of fundamental structural alterations to cope with the new conditions. Some of the modifications which were tried out in the course of geological time proved more successful than others, and as a result we find that old species continuously disappeared and new ones took their places. In consequence of the substitution of certain parts and the complete elimination of others, it is not surprising that living repre-

sentatives are often quite unlike the original stock from which they have descended.

Whales at one time, geologically speaking, were land mammals and, although highly modified in some respects, they still retain all the typical mammalian features. Like land mammals they suckle their young and retain vestiges of their former coating of hair. With the passage of time their fore limbs have been modified to function as pectoral flippers, and their tail has been provided with caudal flukes to function as an organ for propulsion. No traces of hind limbs have been found in any of the living toothed whales with the exception of the sperm whale (*Physeter catodon*), but nevertheless we are fairly certain that these were present in the progenitors of the Cetacea, since the whalebone whales have one or two vestigial limb bones buried deep in the flesh of the pelvic region. Much more profound changes have occurred in the "soft parts" and in the physiological adjustments of their organs to an aquatic life. The bodily organization of living whales shows us what has been accomplished in the way of adaption, but it affords no proof of how this has come about, and for evidence of this sort we must look to the record in the rocks. The skeleton is the framework upon which the muscles and organs are attached, and by studying these "hard parts" and endocranial casts one can infer some of the changes which were taking place in the so-called "soft parts." Porpoises are found in both fresh and salt water, while the whalebone whales are almost exclusively pelagic. Both of these two groups of living cetaceans have followed different paths of anatomical adjustment to fit themselves to this or that manner of living.

To show that adaptation to life in the water is a complex biological transition for a mammal formerly accustomed to land conditions and that such an adaptation has been clearly demonstrated by collateral investigations along the lines of palaeontology, anatomy, embryology, and physiology is the object of this résumé. From the very nature of the evidence it is not surprising that there should be some divergence of opinion as to the details of this biological process, but there is little or no conflict as regards the fundamental principles underlying the views that are based on ascertainable facts.

Some ten years ago the writer was invited to prepare a report on the fossil marine mammals as a part of a research program planned by Dr. John C. Merriam for a study of the extinct vertebrate faunas of the Pacific Coast and Great Basin Provinces of North America, and during the past six years this work has been supported by the Carnegie Institution of Washington. In the course of this investigation the writer has had the opportunity to study the collections of fossil and recent cetaceans in the United States National Museum, the American Museum of Natural History, the Museum of Comparative Zoology, the Museum of Palaeontology of the University of California, and the California Academy of Sciences. In the matter of illustrations the writer has had the able coöperation of Mr. Sydney Prentice, who has prepared practically all of the line drawings used in this essay. In cases where no complete skull has been available the illustration is based on two or more skulls which mutually supplement one another so far as missing parts are concerned, but in each instance the skulls selected for this purpose are conspecific and were obtained from the same geological horizon.

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION

The difficulties that beset one who is engaged in a study of whales, past and present, are in no small measure due to the practically world wide distribution of these pelagic mammals during the Tertiary period and the consequent lack of adeqate material from many parts of their range. Not so many years ago the scope of our geographic knowledge of fossil whales was confined to Europe and North America, but it has been slowly extended until it now includes portions of Africa, South America, Seymour Island in the Antarctic, Australia, New Zealand, and Japan. No remains of fossil whales have as yet been described from continental Asia, nor from the numerous islands which dot the Atlantic, Pacific, and Indian oceans. The imperfection of the geological record is an accepted fact, but probably our knowledge of the past history of the whales would present fewer gaps had a concerted effort been made to assemble systematically collections of fossil pelagic mammals. Marine formations that are known to contain remains of fossil pelagic mammals occur on nearly all continental masses with the exception of Asia. If modern methods of collection and preservation of specimens were applied, many of these marine formations should yield material which would throw additional light on the evolution of this interesting group.

Search for remains of fossil whales has never been prosecuted with the same energy and zeal as for many other orders of vertebrates, and a large number of the forms now known are based on material obtained from thirty to one hundred years ago. Owners of quarries, brick works, marl pits, and diatomaceous deposits have contributed to interested scientists a large part of the fossil whales that have been mentioned in scientific periodicals during the past century. Purely fortuitous circumstances, however, have resulted in the acquisition of some rather large and important collections. When the fortifications of Antwerp were under construction, in the years 1861 to 1863, hundreds of whale skeletons were found in the excavations, and many of them are preserved in the Royal Museum of Natural History at Brussels. As early as 1868 interested officials and employees of the fertilizer companies exploiting the so-called Ashley phosphate deposits of South Carolina noted the extraordinary variety and profusion of fossil remains of vertebrated animals that were brought to light in the course of their operations. Specimens were preserved in company offices and in the homes of interested citizens. In time important collections were built up, and many of these found their way into institutions and museums, where they have been carefully preserved for their scientific value.

Geologically and geographically whales have had a long and widespread range. Some of the living cetaceans are great travellers and apparently wander from one shore to another in the course of their migrations, while others exhibit decided preferences for limited oceanic areas. The extent of the migrations of whales is largely a matter of conjecture, but the evidence points to the conclusion that some species travel from the South Pacific to the North Pacific and vice versa. Sei whales have been taken in Japanese waters with ectoparasites of South Pacific origin (Andrews, 1916). In the Atlantic ocean conditions are similar. Information from other sources indicates that whales pass from one ocean to another around Cape

TABLE 1

Geological and geographical distribution of whales

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	QUATERNARY
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	
ARCHAEOCETI																					
Protocetidae:																					
Eocetus						A															
Pappocetus			?A																		
Protocetus					A																
Prozeuglodon						A	A														
Dorudontidae:																					
Dorudon								N													
Kekenodon											Z										
Phococetus												E									
Zygorhiza							N														
Basilosauridae:																					
Basilosaurus						A	E A–N	E													
ODONTOCETI																					
Agorophiidae:																					
Agorophius								N													
Xenorophus								N													
Squalodontidae:																					
Colophonodon																N					
Metasqualodon													Au								
Microcetus											E										
Microsqualodon													E								
Microzeuglodon													E								
Neosqualodon													E								
Parasqualodon													Au								
Phoberodon													S								
Prionodelphis																		S			
Prosqualodon													S–Z								
Rhytisodon													E								
Saurocetus																N					
Squalodon													E	E–N	N	E–N					
Trirhizodon													E	E							
Iniidae:																					
Anisodelphis																		S			
Hesperocetus																	N				
Ischyrorhynchus																		S			
Pontoplanodes [= *Saurodelphis*]																		S			
Proinia													S								
Ziphiidae:																					
Anoplonassa																N					

Abbreviations: A., Africa; Au., Australia; E., Europe, including Russia; J., Japan; N., North America; S., South America; Z., New Zealand; ?, indicates some uncertainty as to the age or identity; [?], indicates some uncertainty as to family position.

TABLE 1—*Continued*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	QUATERNARY
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Latrorfian	Rupelian	Casselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	
Ziphiidae—*Cont:*																					
Belemnoziphius....																N					
Berardiopsis.....																			E		
Cetorhynchus.....														E		E					
Chonoziphius.....																E–N			E		
Diochotichus.....													S								
Eboroziphius.....																N					
Mesoplodon.....																E–N			E		
Mioziphius.....																E					
Palaeoziphius.....																E					
[?] *Pelycorhamphus*.....																N					
Proroziphius.....																N					
Squalodelphis.....													E								
Ziphioides.....															E						
Delphinidae:																					
Acrodelphis.....													E		N	E					
Agabelus.....															N						
Argyrocetus.....													S								
Belosphys.....															N						
Ceterhinops.....																N					
Champsodelphis....														E	E	E					
Cyrtodelphis [= *Schizodelphis*]...													E–A	E	E–N	E–N	E				
Delphinodon.....															N						
Delphinopsis.....																E					
Delphinavus.....													N								
Delphinus.....																		E	E		
Eoplatanista.....													E								
Eurhinodelphis....															N	E–J					
Globicephala.....																					N
Heterodelphis.....															E	E					
Ixacanthus.....															N						
Iniopsis.....													E								
Kentriodon.....															N						
Lophocetus.....															N						
Macrochirifer.....																E					
Orcinus.....																			E		
Palaeophocaena....																E					
Phocaenopsis.....																					Z
Phocaena.....															E?						
Pithanodelphis....																E					
Pomatodelphis.....														E		N					
Priscodelphinus....															N						
Protodelphinus....													E								

TABLE 1—*Continued*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE			
	Lower			Middle		Upper			Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper	
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Caselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	QUATERNARY
Delphinidae—*Cont.*:																					
Protophocaena....																E					
Pseudorca.....																				E-J	
Rhabdosteus.....															N						
Steno.....																		E	E		
Stereodelphis.....														E							
Tretosphys.....															N						
Tursiops.....														E?				E	E	E	
Ziphiodelphis....													E								
Delphinapterus...																					N
Monodon.....																				E	N
Lonchodelphis....																			N		
Pontistes.....																		S			
Pontivaga.....																		S			
Stenodelphis.....																					N
Platanistidae:																					
Zarhachis.....															N						
Kogiidae:																					
Kogia.....																				J	
Physeteridae:																					
Aulophyseter.....														N							
Balaenodon.....																			E		
Diaphorocetus....													S								
Dinoziphius.....																N					
[?] *Graphiodon*...																N					
Hoplocetus.....														E							
Idiophyseter.....															N						
Idiorophus.....													S								
Ontocetus.....														J	N	N					
Orycterocetus.....															N						
Physeter.....																N		E	E		N
Physeterula.....																E					
Physetodon.....																		Au			
Placoziphius.....																E					
Priscophyseter....																			E		
Prophyseter.....																E					
Scaldicetus.....													?E			E		?Au			
Scaptodon.....													Au								
Thalassocetus....																E					
Incertae sedis:																					
Agriocetus.....												E									
Archaeodelphis...								N													
Patriocetus.....												E									

TABLE 1—*Concluded*

	EOCENE								OLIGOCENE				MIOCENE					PLIOCENE				
	Lower				Middle		Upper		Lower	Middle	Upper		Lower	Middle		Upper		Lower	Middle	Upper		
	Montian	Thanetian	Sparnacian	Ypresian	Lutetian	Auversian	Bartonian	Ludian	Lattorfian	Rupelian	Caselian	Aquitanian	Langhian	Helvetian	Tortonian	Sarmatian	Pontian	Plaisancian	Astian	Sicilian	QUATERNARY
MYSTICETI																					
Cetotheriidae:																					
Amphicetus																		E			
Cephalotropis															N						
Cetotheriomorphus																E					
Cetotheriopsis												E	S								
Cetotherium													?N			E					
Eucetotherium																E					
Heterocetus																		E			
Herpetocetus																E					N
Plesiocetus Auct.													S		E	E					N
Isocetus																E					
Mesocetus														E		E					
Metopocetus															N						N
Pachyacanthus																E					
Pachycetus										E											
Parietobalaena															N						
Plesiocetopsis															N	N		E			
Rhegnopsis															N						
Siphonocetus															N						
Tretulias															N						
Ulias															N						
Balaenopteridae:																					
Balaenoptera																	N	E	E		N
Burtinopsis																			E		
Cetotheriophanes																		E			
Idiocetus																				E	
Megaptera																	N		E		N
Megapteropsis																		E			
Mesoteras																N					
Plesiocetus V.B.																		E			N
Balaenidae:																					
Balaena																		E	E	E	
Balaenotus																			E		
Balaenula																			E		
Eubalaena																					S
Morenocetus													S								
Notiocetus																		S			
Palaeocetus																			E		
Protobalaena																		E			

Horn and Cape of Good Hope. The possibilities for the dispersal of cetaceans are exceptionally great, in view of the absence of physical barriers, and apparently the chief controlling factor is the food supply. Of the thirty genera of living toothed whales, four are restricted to rivers, occurring not only in their estuaries, but occasionally in their tributaries as well. One or two genera, like *Sotalia* and *Steno*, are essentially tropical in their distribution and are represented by one or more species in the Atlantic, Pacific, and Indian Oceans. Many odontocete genera are more widely distributed, and some of them, especially the killer (*Orcinus*), the lesser killer (*Pseudorca*), the common dolphin (*Delphinus*), the sperm whale (*Physeter*), and one of the beaked whales (*Ziphius*) are practically cosmopolitan. The bowhead (*Balaena mysticetus*), which frequents the Arctic seas, and the pigmy whale (*Neobalaena marginata*) of New Zealand waters appear to be restricted in their dispersal by climatic conditions. Some of the whalebone whales are without doubt the largest mammals that have ever lived. No mammal, not even the zeuglodonts, has attained the proportions of the blue or sulphur bottom whale (*Sibbaldus*), individuals of which have measured 98 feet in length. Not all of the living whalebone whales are so large, and one of the smallest is the pigmy whale (*Neobalaena*), which rarely reaches a length of more than 20 feet.

The geological and geographical distribution of whales assembled in table 1 shows many gaps, and the discontinuous distribution in many instances is due either to the inadequacy of the material collected or to lack of effort in areas where material could be secured.

ARCHAEOCETI

The oldest known relatives of the typical cetaceans are found in some of the oldest Tertiary rocks; that is in those that correspond in age to the early part of the Age of Mammals. Even these archaic mammals were well specialized in many respects for a pelagic life. It so happened that the first notice of these mammals was based on a few fragments found in the Eocene of southeastern Caldwell Parish, Louisiana, near the Ouachita River. Dr. Harlan (1834) believed that they belonged to a giant reptile, to which he gave the name *Basilosaurus*, but Owen (1839) was able to demonstrate that they were a part of some colossal mammal, for which he proposed to substitute the name *Zeuglodon*, in allusion to the yoke-like appearance of the cheek teeth. So far as known the oldest zeuglodonts had already acquired a complicated organ for hearing, they retained a well developed olfactory apparatus, but their brain structure as shown by casts indicates that their sight was defective. Although they tried out braincases of somewhat different proportions, the main path of their evolutionary advance seems to have been limited to a remodeling of the cheek teeth. Complete skeletons of the early Eocene zeuglodonts have never been found, but those of the Upper Eocene had lost the functional use of their hind limbs, for the femur was vestigial and the pelvic girdle atrophied.

It is neither desirable nor possible to recount in detail here the various views that have been advanced regarding the affinities of the zeuglodonts. In recent years the concept that they are related to if not descended from the primitive insectivore-carnivore stock has had wide acceptance. Morphologically they seem relatively near to the typical whales and porpoises, although it is not necessary to assume that any known zeuglodont is ancestral to some particular kind of whale, for the zeuglodont skull in its general structure appears to be divergent from

rather than antecedent to the line of development that led to the telescoped condition of the braincase seen in skulls of typical cetaceans. On the contrary it is more probable that they are collateral derivatives of the same stock from which the true Cetacea sprang. No tendency toward cranial telescoping has been observed in any of the zeuglodonts, yet they possess certain structural features which are morphologically intermediate between early land mammals and true cetaceans. Miller (1923) holds that the known zeuglodonts are not directly ancestral to any of the recent whales, and contends that the transition from this type of skull to the toothed whale (Odontoceti) skull involves simpler principles than is the case for the whalebone (Mysticeti) whales. Curiously enough, periotic bones of both the whalebone and the toothed whale types have been found attached to skulls of zeuglodonts.

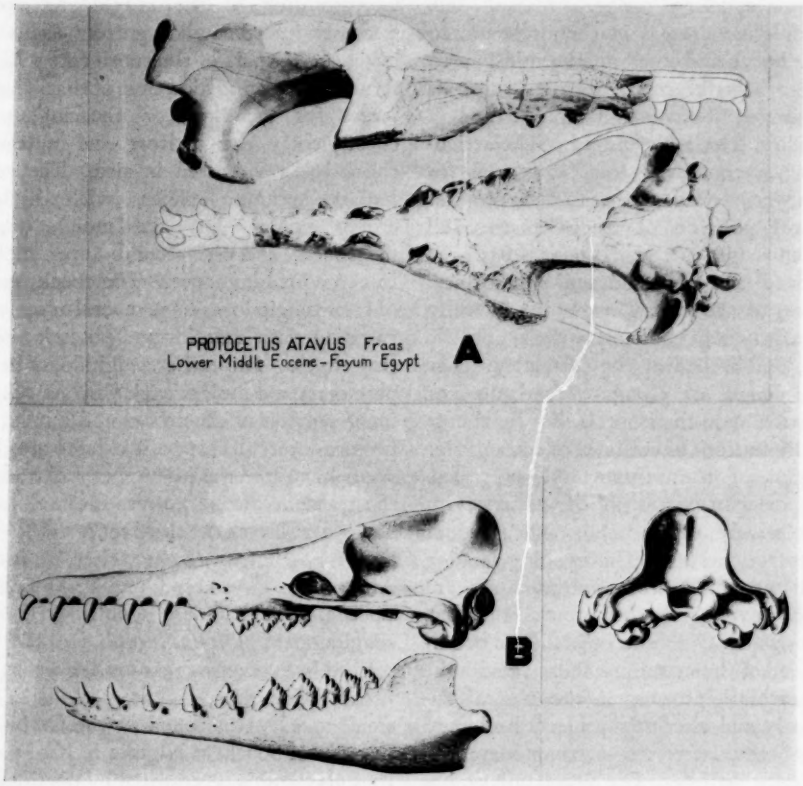

FIG. 1. SKULLS OF ZEUGLODONTS

A. Dorsal and ventral views of skull of *Protocetus atavus* (after Fraas). *B*. Lateral and posterior views of skull of *Prozeuglodon stromeri* (after Stromer).

The bones in the rostrum and cranium of

these zeuglodonts retain their normal mammalian relationships; the facial region is elongated without overlapping of the bones. The braincase is narrow and elongate, and not shortened antero-posteriorly as in living whales, for all have a remarkable elongated intertemporal constriction and large temporal fossae. The parietals are normal in their relation to other bones and meet on the mid-line to form a sagittal crest. The exoccipitals are already extended laterally, and a lambdoid crest is developed. The articular surface on the zygomatic process for the lower jaw tends to assume the peculiar vertical position of true Cetacea. All known zeuglodont skulls have a flattened forehead and a broadened supraorbital process of the frontal, extended laterally beyond the jugal portion of the zygomatic arch, and arched at the extremity. The nasal bones are elongated and do not encroach upon the frontals, but lie almost wholly in front of the level of the anterior margins of the supraorbital processes. The posterior portion of the nasal cavity is relatively undisturbed, and turbinal bones are present. The opening leading to the nostrils has been moved backward to the level of the first upper premolar, about halfway to the orbit. The proximal end of the maxillary abuts against the supraorbital process of the frontal superiorly and inferiorly projects backward below the latter to accommodate the posterior molars. The premaxillary has an ascending process which does not reach the frontal, but terminates behind the antorbital foramen (above Pm^2 or Pm^3) and anteriorly is conspicuously extended beyond the extremity of the maxillary. Apparently the mouth was used mainly as a pair of forceps, with long, narrow, beak-shaped rostrum, in which the anterior teeth are widely spaced. The incisive foramina were eliminated by the linear contact of the premaxillaries along the mid-line. The palatines do not extend forward beyond the level of the posterior premolar, but the bony palate is prolonged backward by outgrowths of the palatines and pterygoids. The tympanic bulla has already acquired an involucrum. If our interpretation of the zeuglodont skull is correct, a somewhat greater use was made of that part of the tooth row which serves for grasping food than of that which serves for grinding, or shearing, and consequently the incisors and anterior cheek teeth increased in size. The premolars became heavier, with higher crown points, but the molars were weakened, and the second upper molar lost its predominance. The cheek teeth of later zeuglodonts have several accessory cusps on their anterior and posterior cutting edges. The earlier zeuglodonts have premolars and molars with vestiges of the inner portion of the crown and a reduced postero-internal cusp. The later zeuglodonts have lost the last upper molar, and the remnant of the postero-internal cusp disappeared with the third root.

So far as known to the writer, no fossil Archaeoceti have been found in the Lower Eocene, though it is not unlikely that a zeuglodont, *Pappocetus lugardi*, recently described by Andrews (1920) will eventually prove referable to that period. This small species was found in the Ombialla District of Southern Nigeria in hard pyritous clay and is represented by portions of two left mandibles belonging to immature individuals, for the last molars are not cut in either specimen. The mandibles of this zeuglodont apparently possessed the full eutherian dentition, with 3 incisors, 1 canine, 4 premolars, and 3 molars in each lower jaw, and it is especially interesting on account of the carnivore-like characters of the cheek teeth. The premolar-molar series, with the exception of the first lower

premolar, possess a well defined cingulum and retain distinct vestiges of the inner portion of the crown. The premolars have a crown with one large cusp and a rudimentary basal posterior cusp. The fourth lower premolar has the longest antero-posterior diameter. Each of the three molars has a large anterior cusp and a smaller posterior cusp. In contrast to zeuglodonts of later stages the second incisor is relatively large.

In passing from the lower Middle Eocene to the uppermost Eocene, zeuglodonts are encountered which reveal some of the progressive stages in the remodelling of the cheek teeth as well as the reshaping of the occipital region of the skull and other skeletal changes.

Several faunas of these zeuglodonts have been discovered in the Middle and Upper Eocene deposits of the Fayum in Egypt. These rocks are older than our own Gulf Coastal Plain deposits and have yielded several rather distinct types of zeuglodonts. The oldest geologically is a somewhat generalized form, *Protocetus atavus*, described by Fraas in 1904, from the basal member of the Lower Mokattam stage near Cairo. The skull of this small species is less than two feet in length and bears little resemblance to living cetaceans. The normal eutherian dentition is present. In common with the oldest land mammals, there is a marked difference between the anterior grasping teeth and the posterior cutting teeth. In contrast to zeuglodonts of later stages of the Eocene, the teeth of *Protocetus* do not bear step-like cusps on their anterior and posterior cutting edges, and distinct vestiges of the inner portion of the crown are retained. The two posterior upper premolars and the three molars have three roots and a remnant of the postero-internal cusp. Both Fraas and Andrews have pointed out that *Protocetus* is a highly important link in the history of the Archaeoceti, for here we have a skull that is typically zeuglodont in general form combined with a dentition that is essentially that of a creodont. In some characters, such as the peg-like odontoid and the relatively long centrum, the axis of the lower Middle Eocene *Protocetus* approaches the type of cervical found in the carnivores. The late Dr. C. W. Andrews of the British Museum of Natural History contended that the zeuglodonts probably originated on the northern shores of Africa in the early part of the Tertiary period and that *Protocetus* was an annectant form between the later zeuglodonts and the earlier creodonts.

In the upper Middle Eocene a slightly more advanced type of zeuglodont, *Prozeuglodon atrox* (Andrews, 1906) makes its appearance. It should be noted here that Professor Stromer (1908) has suggested that this may be a young individual of *Zeuglodon isis*. The skull of this species measures about 26 inches in length, and the occipital shield has the appearance of being less constricted above the condyles. The number of molars is uncertain, but otherwise it has the normal eutherian dentition. The cutting edges of the crowns of the molars and the three posterior premolars are serrated. Pm.^{3}, Pm.^{4}, and M.^{1} have an enamel covered buttress, evidently the remnant of the postero-internal cusp, and in the premolars at least this buttress is supported by a distinct third root. *Prozeuglodon* has an axis with a short, blunt, rounded odontoid, while that of "*Zeuglodon*" is flattened above. Zeuglodonts of the Upper Eocene have an axis with a high massive neural spine, but the centrum and transverse processes are shortened. The evidence appears to be fairly clear that a shortening of the neck was brought about by a reduction of the centra of the cervical

vertebrae. A similar history is known for living cetaceans. *Prozeuglodon stromeri* is the representative of this series in the Upper Eocene. A fairly complete skeleton (Stromer, 1908), measuring about ten feet in length including the skull, which measures 28 inches, gives us a fairly adequate conception of this species.

Several diverse types of zeuglodont skulls, which appear to belong to four distinct series, have been found in the Upper Eocene. "*Zeuglodon*" *osiris* (Stromer, 1903) is probably the best known of the small zeuglodonts that make their appearance subsequent to the lower Middle Eocene. The skull of this species did not exceed 30 inches in length. The braincase is narrow, elongated, and high posteriorly, and the bones in the cranium retain their normal mammalian relationships. The skull of "*Zeuglodon*" *osiris* is remarkable for the narrowness of its occipital shield, the lateral portions of the lambdoid crest being sharply deflected backward so that this surface has the appearance of being constricted above the condyles. These modifications afford an increase in surface for attachment of jaw muscles and no doubt are correlated with increasing size and strength of the mandible. As compared with "*Zeuglodon*" *intermedius* the condyles and foramen magnum are smaller, the rostrum seems to be narrower, and perhaps the opening leading to the nostrils was situated farther back. In this series there is a tendency toward a narrowing of the occipital shield accompanied by a folding back of the lambdoid crests, resulting in increasing concavity of the surface above the foramen magnum. The sagittal crest increases in height, and the condyles and foramen magnum diminish in size. The cheek teeth of these two zeuglodonts are serrated on their anterior and posterior cutting edges, and the last upper molar is lost. According to Andrews (1923) the buttress or postero-internal cusp is reduced in size and apparently was not supported by a third root.

The depression of the occipital shield in the *Zygorhiza minor* series was accompanied by decreasing convexity of the lateral cranial walls and a rather pronounced folding backward of the lambdoid crest. This crest is exceptionally high and flaring, and is raised from 30 to 40 mm. above the lateral walls of the braincase. The rostrum has increased in length and slenderness, and the opening leading to the nostrils has moved farther backward, the interval between it and the orbit being about one-third the length of the rostrum. In *Zygorhiza minor* (Müller, 1849, and True, 1908), however, both ends of the premolar-molar series appear to have been reduced, inasmuch as the first upper single-rooted premolar and the third upper molar are missing on the cast of the type skull obtained from the Tyler museum. The first tooth of the upper premolar series of "*Zeuglodon*" *zitteli* according to Stromer (1903, p. 82) is likewise two-rooted. In the smaller zeuglodonts, such as *Zygorhiza minor* and *Prozeuglodon stromeri* (Stromer, 1908, No. Mn. 9, p. 110, pl. 4), the skull equalled approximately one-fifth of the total length of the skeleton, but in the colossal types like *Basilosaurus cetoides* not more than one-tenth of the total length.

The carnivorous zeuglodonts typified by *Basilosaurus cetoides* (Gidley, 1913) of the Gulf Coastal Plain of the United States, which attained a length of from 50 to 70 feet and whose skull measured approximately 5 feet in length, reached the flood tide of their evolutionary advance during late Eocene times. It seems to be generally conceded that gigantism is one of the indications of approaching extinction, but there must have been other contributing factors, for the Oligocene

zeuglodonts were much smaller and represent another line of descent. In later Eocene zeuglodonts the dentition is reduced by the loss of the third upper molar. The elimination of the postero-internal cusp of the cheek teeth was followed or accompanied by the loss of the third root. In the case of *Basilosaurus cetoides* of North America as well as "*Zeuglodon*" *isis* (Stromer, 1908) of the Fayum the cheek teeth have not more than two roots, and not even a vestige of the postero-internal cusp remains. The cheek teeth have a laterally compressed crown, that of the premolars serrated on both edges and that of the molars on one or both edges. The shoulder blade is cetacean-like, but the humerus has held more closely to the original form, retaining a well developed deltoid ridge, greater and lesser tuberosities, and a hinge-shaped distal articular surface. The sternum is relatively large and is made up of several sections. At least two of the small zeuglodonts, *Zygorhiza minor* and *Prozeuglodon stromeri*, have lumbar vertebrae with short centra and long articulating zygapophyses, while the large *Basilosaurus cetoides* and "*Zeuglodon*" *isis* have lumbars with greatly elongated centra, although the neural arches have remained short. This specialization is unique among mammals, for the greater part of the vertebral column is articulated only by the centra, the zygapophyses being separated by too wide an interval to function in the normal manner.

The short bodied zeuglodonts, such as *Zygorhiza minor*, which have a short neck, thoracic and lumbar vertebrae with high, broad neural spines, well developed transverse processes, and articulating zygapophyses, must have had a propelling mechanism of considerable strength, for among living cetaceans the most powerful swimmers have a vertebral column of this type. The conclusion can be drawn that these short bodied zeuglodonts propelled themselves by upward and downward strokes of the flukes, after the manner of living whales. They were therefore undoubtedly powerful swimmers, capable of diving or turning at will, and were equipped with a dentition admirably fitted for seizing and holding their prey.

Conversely the gigantic zeuglodonts, such as *Basilosaurus cetoides*, which have an elongated trunk and tail, the neck conspicuously shortened, thoracic and lumbar vertebrae with low neural spines and short transverse processes disproportionate to the length of the skeleton, and zygapophyses of all the trunk vertebrae with the exception of the first four or five dorsals, separated by increasing intervals proportional to length of centrum, could hardly have had a powerful propelling tail operating in the same fashion. On the contrary these details indicate that the tail was adapted for lashing, and that in swimming the animal progressed by marked sinuous or serpentine movements.

By the close of the Eocene period zeuglodonts had spread widely, for their remains have been found in Russia, England, and other localities in Europe, the Atlantic and Gulf Coastal plains of the United States, New Zealand, and Seymour Island in the Antarctic. A few of the smaller forms held over until near the close of the Oligocene.

TYPICAL CETACEA

The conclusion that cetaceans living and extinct have arisen from a multiserial stock appears to be borne out not only by osteological, but also by anatomical evidence. That at least three distinct lines of descent are represented among the known Cetacea is evidenced by the general acceptance among mammalogists of the three suborders, of which the Archaeoceti or zeuglodonts at present are known to

have been in existence at a more remote time than the Odontoceti or toothed whales; while the known geological history of the Mysticeti or whalebone whales is much shorter and does not date at present farther back than the Oligocene. The exigencies of an aquatic mode of living are such that the members of the several families of these three suborders assumed a similar outward appearance in conformity with streamline requirements such as have been forced upon many other unrelated groups of aquatic vertebrates, but there is no palaeontological evidence to support any assumption of a remodeling of originally unlike parts to a similar adaptive use. The directions in which the members of these three suborders, collectively and individually, subsequently developed were predetermined by peculiarities of structure in existence at or before the entrance upon a pelagic habitat. The resemblances between these three suborders are such as to suggest a rather close relationship of the original ancestral forms and common descent from some broad headed ancestral stock in which the critical cranial elements were united by squamous instead of dentate sutures. No extinct cetacean skull known holds proof of descent of an archaic toothed whale from any known zeuglodont, or presents structural conditions necessary to form the basis for the elaboration of the mysticete and odontocete types of skull from any common cetacean stock.

A mammalian skull is composed of a number of distinct bones, some of which build up a closed box to protect the nervous system; on the lower posterior bones of the skull are located the articular surfaces for the supporting atlas vertebra of the neck and the bones of the tongue, while others make up the jaws and the muzzle portions. The exposed surfaces of the several bones give origin to or afford insertion for the various muscles which are found in the region of the head. In the generalized type of skull, such as may be found in some of the early Tertiary land mammals, the individual bones exhibit certain mutual contact relationships, and this original architectural plan has been retained with few exceptions during the Cenozoic era by most orders of mammals. Changes in the relative size and shape of the individual bones occur frequently in the geological history of most groups, but there has been very little rearrangement of the bones themselves. Skulls of cetaceans other than zeuglodonts differ from those of all land mammals in that they exhibit an extreme type of remodeling and present alterations which have affected not only the relative size and shape of many of the individual bones, but also their mutual relations. Except for the zeuglodonts, the skulls of all known cetaceans show in some degree the effects of telescoping—that is, the braincase or the portion of the skull behind the rostrum has been shortened, mainly by the slipping of one bone over another or by interdigitation. Gerrit S. Miller (1923) has discussed the telescoping of the cetacean skull in considerable detail and has shown that this process proceeded according to two different plans, one of which is found in the whalebone whales (Mysticeti) and the other in the toothed whales (Odontoceti).

The departure from the generalized type of land mammal skull is most striking in living cetaceans, but even in the earliest known extinct genera of true whales (*Agorophius*, *Xenorophus*, and *Archaeodelphis*) the telescoping was well advanced. If the zeuglodonts and the archaic toothed whales did arise from terrestrial mammals during the Lower Eocene stage, then the rapidity with which they became so completely adapted for an aquatic life far

FIG. 2. SKULL OF BALAENOPTERA BOREALIS, YOUNG MALE, WALNUT POINT, VIRGINIA

A. Dorsal view. *B*. Lateral view. *C*. Lateral view of disarticulated skull, with rostrum and occipital shield detached. *D*. Lateral view of disarticulated skull, with frontal and vomer detached from braincase; the rostrum has been removed. The following abbreviations are used on the text figures: *Al.*, alisphenoid; *Al. gr.*, alveolar groove; *Ant. n.*, antorbital notch; *Ap. max.*, apophysis of maxillary; *As. pr.*, ascending process of maxillary; *Bo.*, basioccipital; *C.*, condyle; *Ect.*, ectethmoid; *Ex. oc.*, exoccipital; *f. inf.*, infraorbital foramen; *f. max.*, maxillary foramen; *f. olf.*, olfactory foramen; *f. pmx.*, premaxillary foramen; *Fr.*, frontal; *Inf. pr.*, infraorbital process of the maxillary; *Ju.*, jugal; *La.*, lachrymal; *Max.*, maxillary; *Max. cr.*, crest of maxillary; *Max. inc.*, maxillary incisure; *Max. t.*, maxillary tuberosity; *Mst.*, mesethmoid; *Mxc.*, ossified mesorostral cartilage; *Na.*, nasal; *Pa.*, parietal; *Pal.*, palatine; *Pmx.*, premaxillary; *p. max. f.*, posterior maxillary foramue; *Prs.*, presphenoid; *Pt.*, pterygoid; *S. oc.*, supraoccipital; *S. or. pr.*, supraorbital process of frontal; *Sq.*, squamosal; *Vo.*, vomer; *Zyg.*, zygomatic process of squamosal.

surpassed evolutionary changes in contemporary land dwelling carnivores. The future will show, I believe, that the geological history of the odontocetes and mysticetes is considerably longer than some investigators have conceded.

Returning to telescoping as a factor in the remodeling of the cetacean skull, we find that one of the earliest and most obvious results of this general evolutionary trend was the reduction and virtual elimination of the intertemporal region. This was not accomplished by the elimination of elements in the cranial region, but by the elongation of certain bones and the slipping of others over those with which they at one time met edge to edge in sutural union. In one group, the Odontoceti, there has been an elongation of the proximal portion of the maxillary and in the other, the Mysticeti, an elongation of the supraoccipital. In the first group there has been a backward overthrust of anterior cranial elements and in the second a forward overthrust of posterior cranial elements. While this general tendency in direction of the thrust prevails in most of the odontocetes under consideration, types also exist in which the backward and forward overthrusts are combined in such a way as to give rise to a more or less balanced condition of telescoping, such as is found in the physeteroids, while in the ziphioids the primary backward maxillary overthrust apparently was stopped abruptly by a final forward occipital thrust.

There is one fundamental difference in construction between the whalebone and the toothed-whale type of skull, and this feature may account for the different structural modifications that characterize these two living groups of cetaceans. In skulls of whalebone whales (Mysticeti), the maxillary can not overspread the braincase because its posterior extremity straddles the supraorbital process of the frontal in the form of two processes, the lower of which is known as the infraorbital and the upper as the ascending process. The upper surface of the expanded supraorbital process of the frontal is left bare and the relatively narrow ascending process of the maxillary is mortised into the body of the frontal behind the level of the narial passages. The infraorbital process of the maxillary lies beneath the anterior border of the inferior surface of the supraorbital process of the frontal and projects conspicuously behind and beneath the infraorbital foramen. It is quite obvious that any backward movement of the maxillary would be retarded by this interlocking with the supraorbital process of the frontal, but the impetus for telescoping was not to be blocked by any such impediment. Inhibited by what appear to be insurmountable obstacles at the base of the rostrum, the direction of the thrust was reversed from backward to forward. This forward overthrust of the elongate occipital shield carried the posterior and intertemporal elements forward, bringing the apex of the supraoccipital to or beyond the median interorbital level and forcing the parietal to override the frontal above the base of the supraorbital process, in some instances as far forward as the level of the proximal end of the nasal (*Balaenoptera acuto-rostrata*, *B. physalus*, and *B. borealis*).

In the toothed whale (Odontoceti) type of skull, as heretofore mentioned, the direction of the overthrust of the cranial elements has been mainly toward the rear. The entire proximal portion of the maxillary is pushed back over the supraorbital process of the frontal to meet or approach the supraoccipital at the level of or behind the orbit; laterally this bone spreads out and, together with the

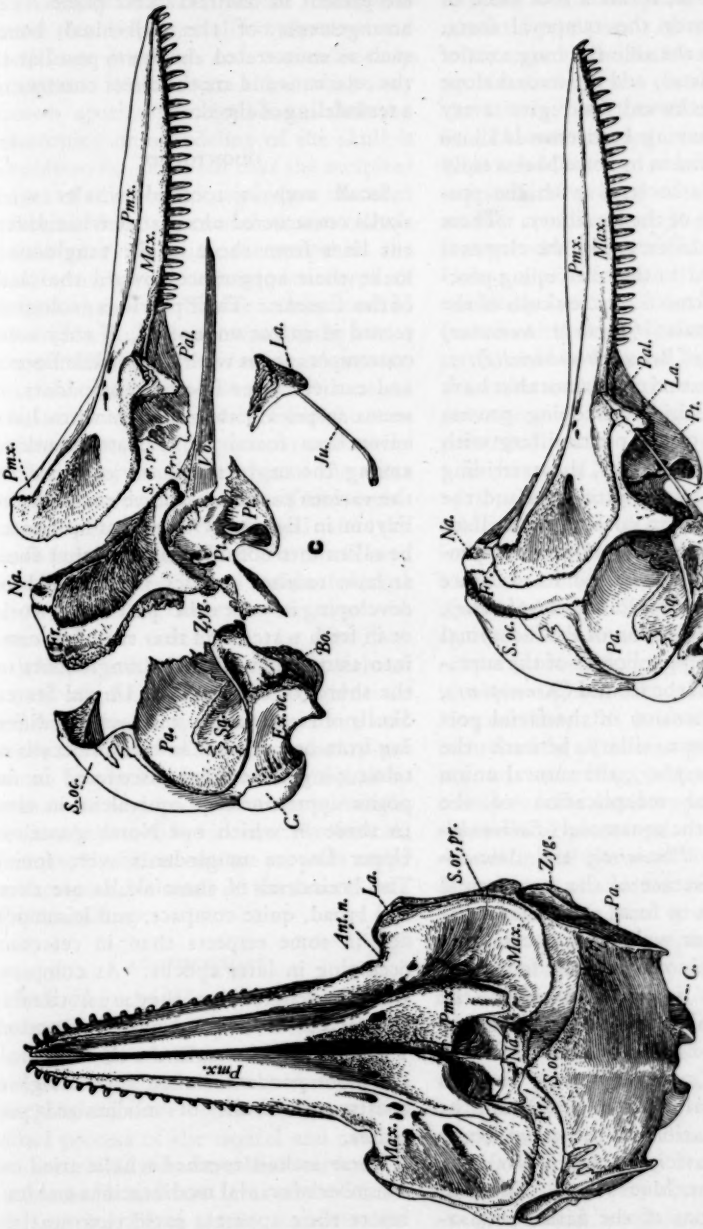

FIG. 3. SKULL OF TURSIOPS TRUNCATUS, HATTERAS, NORTH CAROLINA

A. Dorsal view. *B*. Lateral view. *C*. Lateral view of disarticulated skull, with braincase and rostrum detached.

thin underlying lateral plate-like extension of the frontal, forms a roof more or less complete over the temporal fossa. As viewed from the side the long axes of the frontal, parietal, and squamosal slope upward and backward, and give every appearance of having been crowded into their present position by some backwardly delivered force associated with the posterior overthrust of the maxillary. These opposite trends of thrust in the elements chiefly concerned in the telescoping process may be illustrated by the skulls of the bottlenose porpoise (*Tursiops truncatus*) and the Sei whale (*Balaenoptera borealis*).

Among the unusual conditions that have arisen through this telescoping process are the contact of the premaxillary with the supraoccipital (*Kogia*), the overriding of the palatine by the pterygoid and the contact of the latter with the maxillary (*Platanista*), the antero-posterior expansion of the alisphenoid and its contact with the supraoccipital (*Aulophyseter*), the backward projection of the lachrymal along the outer upper border of the supraorbital process of the frontal (*Xenorophus*), the outward extension of the facial portion of the premaxillary beneath the maxillary (*Xenorophus*), the sutural union of the external reduplication of the pterygoid with the squamosal (*Eurhinodelphis*, *Zarhachis*, *Platanista*, and *Stenodelphis*), the coalescence of the mesethmoid and ectethmoids to form a flattened bony plate on anterior wall of braincase over the greatly reduced frontal fontanelle (practically all living delphinoids), the wing-like lateral extension of the vomer which is applied to the ventral surface of the maxillary (young *Physeter*), the loss of the right nasal bone (*Physeter*), and the close approximation of the nasal bones with the supraoccipital (*Sibbaldus*). In the case of the blue whale (*Sibbaldus musculus*) portions of the nasal, premaxillary, maxillary, parietal, and frontal are present in one transverse plane. Rearrangements of the individual bones such as enumerated above are peculiar to the cetaceans and are the direct outcome of a remodeling of the skull.

ODONTOCETI

Small archaic toothed whales with skulls constructed along somewhat different lines from those of the zeuglodonts make their appearance toward the close of the Eocene. Their previous geological record is as yet unknown. If they were contemporaneous with the Middle Eocene and earlier Upper Eocene zeuglodonts, it seems surprising that their remains have never been found or at least identified among the many specimens obtained by the various parties that have explored the Fayum in Egypt. Other possibilities to be taken into consideration are that these archaic toothed whales may have been developing in some other part of the world or in fresh water, and that they first came into association with the zeuglodonts on the shores of the southern United States. Skulls of two of these small whales differing from one another in certain details of telescoping have been discovered in deposits approximately equivalent in time to those in which our North American Upper Eocene zeuglodonts were found. The braincases of these skulls are short and broad, quite compact, and less modified in some respects than in cetaceans occurring in later epochs. As compared with the zeuglodonts, they are noticeably contracted in a fore-and-aft direction. The individual bones in the skull as a rule are more ponderous than in the lighter constructed skulls of modernized porpoises.

These archaic toothed whales tried out a number of cranial modifications and long before their apparent extinction near the

close of the Oligocene they had attained a high degree of specialization. The characters retained, especially in the skull and teeth, are primitive and not sufficiently diagnostic to connect them with any known species of zeuglodont, and the telescoping or remodeling of the skull is already so far advanced that the incipient stages of this general process are obscured by certain details of cranial construction.

One may visualize the steps in the transformation of a zeuglodont type of skull to that of the Eocene archaic toothed whale, but skulls demonstrating the actual stages have never been found. Assuming that the skulls of these archaic toothed whales have been derived from the zeuglodont type of skull, one must necessarily concede that the outer edge of the maxillary immediately in front of the supraorbital process of the frontal and the tooth-bearing portion of the maxillary, which projects backward beside the jugal below the orbit, must degenerate or be eaten away in order that the maxillary may be pushed back over the supraorbital process of the frontal. The jugal must lose its connexion with the maxillary and fuse to the ventral surface of the lachrymal bone. The lachrymal bone must continue to retain its position at the anterior margin of the supraorbital process of the frontal, but must be shifted so that it comes to lie on the ventral instead of the lateral face of the maxillary.

AGOROPHIIDAE

Skulls of the Upper Eocene genera *Xenorophus* and *Agorophius* conclusively show that the maxillary and premaxillary have been subjected to a backward thrust, which forced these bones over the supraorbital process of the frontal and carried the antorbital foramen backward until it came to lie near the level of the antorbital notch. These skulls, however, do not give us any clew as to how this slipping was accomplished. By referring to text figure 4 one can see at a glance in what respects the backward thrust of the proximal end of the rostrum has changed the relative positions of certain elements. In all known zeuglodont skulls the maxillary straddles the anterior face of the supraorbital process of the frontal in a manner comparable to that existing in the living whalebone whales (Mysticeti). Unless the infraorbital portion of the maxillary atrophied and finally disappeared with the reduction of the molar teeth, and we have no direct evidence to show that such was the case, no backward movement of the maxillary would be permitted.

In the case of *Xenorophus sloanii* (Kellogg, 1923), the maxillary is excluded from the orbital region by the combined jugal and lachrymal. The lachrymal bone has already assumed a position typical of toothed whales (Odontoceti), abutting against the anterior border of the supraorbital process of the frontal and mortised into the ventral face of the maxillary. Nevertheless, this bone differs from the lachrymal in all known porpoises in having an ascending process, which has overspread the outer upper border of the supraorbital process of the frontal. The remodeling of the skull has proceeded in directions that have not been followed by odontocetes of later geological stages. Some inexplicable peculiarity in the skull of an immediate precursor gave rise to unusual conditions in the *Xenorophus* skull, which differs from all other known cetaceans in having the premaxillary widened posteriorly so that it extends conspicuously outward underneath the maxillary over the basal half of the supraorbital process. Furthermore, the maxillary slopes very abruptly in front of the antorbital notches. Although the

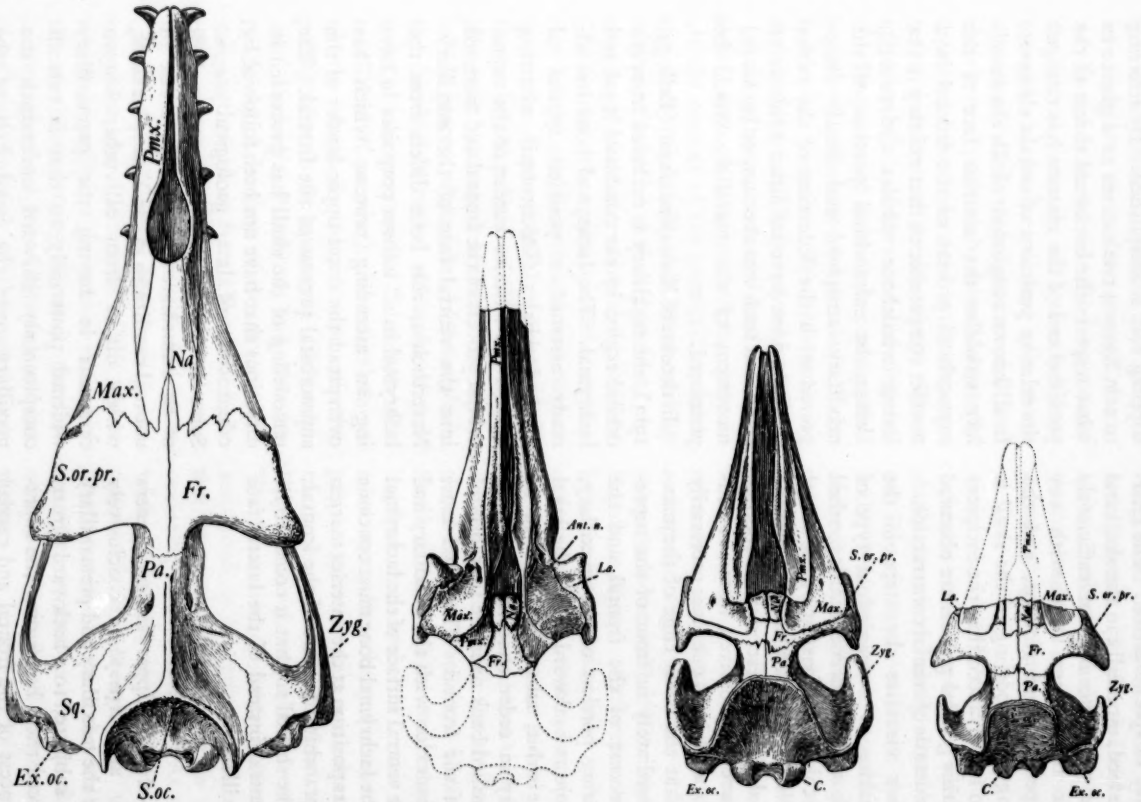

FIG. 4. DORSAL VIEWS OF UPPER EOCENE SKULLS

Prozeuglodon stromeri, Qasr-el-Sagha stage, Fayum, Egypt. *Xenorophus sloanii*, Ashley marl, South Carolina. *Agorophius pygmaeus*, Ashley marl, South Carolina. *Archaeodelphis patrius*, (?) Ashley marl, South Carolina.

skull of *Xenorophus* has a rather elongated rostrum, it differs from the zeuglodont skull in having the opening leading to the nostrils located behind the level of the anterior margin of the orbit. The nasal bones are noticeably shortened, and their bases are mortised into the frontals near the level of the posterior margin of the orbit. The palatine bones of this skull extend forward beyond the antorbital notches, and there is no evidence that their position with respect to other basicranial elements was affected to any marked extent by the backward thrust of the maxillary. The posterior extremity of each palatine abuts against the corresponding edge of the pterygoid and, unless they were permitted to slide under the latter, they would remain in approximately their original positions, but a telescoping of these elements has occurred in some of the living porpoises, for in *Mesoplodon* the palatines are largely overspread by the greatly enlarged pterygoids, while in *Platanista* the palatines are greatly reduced and are completely overspread by the pterygoids.

The idea that the skull of the Upper Eocene *Agorophius pygmaeus* (Leidy, 1869; True, 1907) bore some resemblance to the rorquals apparently originated with Paul Gervais (1871), and Cope (1895) remarked that if teeth were absent it would be necessary to refer this cetacean to the Mysticeti. The possibility that *Agorophius* may be one of the direct ancestors of the whalebone whales (Mysticeti) appears to be excluded, in view of the limitations imposed by the actual mechanical construction of the skull. In *Agorophius* the maxillary broadly overspreads the supraorbital process of the frontal and does not stop in front of or project backward beneath it, as in all known Mysticeti. On the contrary in skulls of both fossil and living whalebone whales the proximal end of the maxillary as seen from a dorsal view abuts against the supraorbital process of the frontal for most of its width, but is attached to the frontal in the interorbital region by a narrow ascending process. Once inaugurated it is difficult to conceive how the general process of telescoping could be reversed, since the backward slippage of the maxillary depends upon the removal of an obstruction consisting of the infraorbital portion of this bone, a process furthermore that is retained by all known whalebone whale skulls. Any assumption that the mysticete skull was derived from an *Agorophius* type necessitates a reversal of the impetus that led to the backward thrust of the proximal rostral elements in addition to a secondary development of an interlocking maxillary. To accomplish this the broad plate of the maxillary which already has overspread the supraorbital process must be reduced to a narrow ascending process and a broad infraorbital process must arise.

The association of *Agorophius* with the odontocetes rests on a much sounder basis, for this archaic toothed whale undoubtedly represents a somewhat distantly related precursor of the squalodonts, which include a number of diverse types. There is reason to believe that *Agorophius* at least represents a morphological stage through which the toothed whales may have passed in their development and that the subsequent remodeling of the odontocete cranium was accomplished by a forward movement of the occipital region until the supraoccipital shield came in contact with the frontals. Additional support to the view that the parietals were crowded out by some forward movement of the posterior elements is to be found in skulls of immature bottlenosed porpoises (*Tursiops truncatus*), in which the parietal bones form the outer upper border

Prosqualodon stromeri, Qasr-el-sagha stage, Fayum, Egypt. *Xenorophus sloanii*, Ashley marl, South Carolina. *Agorophius pygmaeus*, Ashley marl, South Carolina. *Archaeodelphis patrius*, (?) Ashley marl, South Carolina.

of the so-called occipital shield and are broadly overspread by the supraoccipital.

It would appear that the archaic toothed whales and the zeuglodonts, which had dominated the later Eocene seas, dwindled in numbers almost to the point of extinction by the close of the Oligocene. So far as the record shows, an extraordinary transformation of the odontocete skull took place in the interval of time preceding the beginning of the Miocene, which seemingly swept forward with prodigious rapidity, for several families had already acquired their peculiar details of structure by that time. Nevertheless one must not forget that the developmental history of the toothed whales during the Lower and Middle Oligocene is wholly unknown and that there is a surprising scarcity of described forms from the Upper Oligocene. The archaic toothed whales seem to have given rise to the squalodonts, which were the forerunners and perhaps the direct ancestors of the primitive ziphioid and iniid porpoises. These squalodonts continued through the Miocene, attaining their highest development, but perhaps not their greatest size. The sudden arrival of delphinoids with highly telescoped skulls as well as physeteroids with depressed braincase and characteristic postrostral basin in the Lower Miocene is the most startling evidence in favor of a rapid remodeling of the archaic toothed whale type of skull during the Oligocene, if it can be shown that they are derivatives of the later Eocene stock of true whales. One would hardly anticipate so radical a remodeling of a generalized type of skull in the course of one geological period.

The assemblage of toothed whales, which begin their career in the Lower Miocene, includes at least five of the recognized families of odontocetes. These families may be listed according to their specialization as follows: Squalodontidae, Iniidae, Ziphiidae, Delphinidae, and Physeteridae. Even in the skulls of these early Miocene porpoises the passages leading to the nostrils have been pushed backward to the level of the eyes and the choanae are nearly vertical, an adaptation for breathing in the water. The postorbital constriction has been eliminated on the skulls of all of these extinct porpoises, and the frontal bones are in contact posteriorly with the supraoccipital. The skulls of all known Miocene porpoises are constructed along the same general mechanical lines as those now living, although their rostra may assume quite different proportions. A noticeable tendency toward the lengthening of the rostrum is evidenced in many of the Miocene genera, and this process seems to culminate in the late Miocene or early Pliocene. Porpoises with moderately elongated rostra, actually much shorter than the peculiar Miocene porpoises hereinafter discussed, are found in the existing pelagic faunas, but it was not until the later Miocene that the true short-snouted porpoises made their appearance. The history of the several families of toothed whales may be traced briefly and the typical features of their respective groups illustrated by selected genera.

SQUALODONTIDAE

The oldest known faunas of pelagic mammals of the Lower Miocene appear to be those obtained from the Patagonian marine formation on the coast of Chubut Territory, Argentine Republic, and the sand pits of Libano and Bolzano, near Belluno, in the Province of Venetia, Italy. Among the peculiar types of extinct whales found in these formations are the shark-toothed porpoises, *Prosqualodon australis* (Lydekker, 1894), *Pho-*

berodon arctirostris (Cabrera, 1926), *Squalodon bariense* (Dal Piaz, 1916), and *Squalodon bellunense* (Dal Piaz, 1916). Porpoises of this type have been called squalodonts because of the general similarity between their teeth and those of sharks; but the teeth of squalodonts, unlike those of sharks, have two or three roots. These squalodonts must trace their ancestry back to unknown small archaic toothed whales of the Eocene, having teeth of similar shape and skulls of an antecedent construction. It is obvious that the narial passages have moved farther back than in their Eocene predecessors; the nasal bones are very much atrophied and are pressed into the frontals on the forewall of the braincase. In addition to other peculiarities possessed by these skulls, there are two small apertures on the anterior wall of the braincase for the passage of olfactory

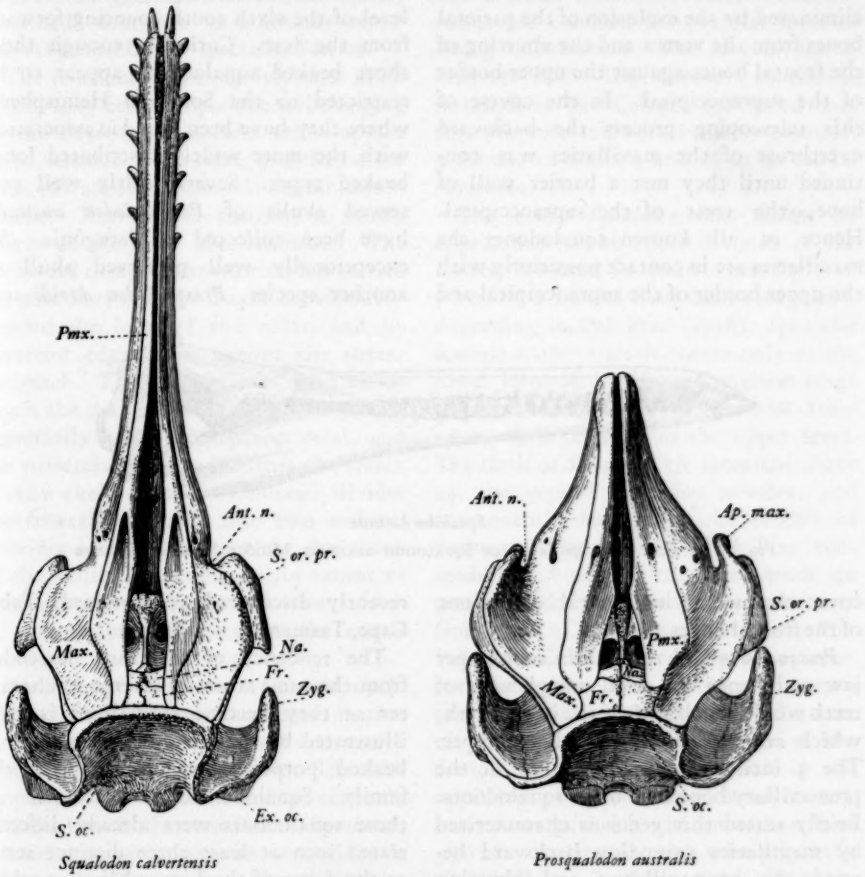

FIG. 5. DORSAL VIEWS OF SKULLS
Prosqualodon australis, Lower Miocene, Patagonia. *Squalodon calvertensis*, Middle Miocene, Maryland

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nerves leading to the "blow hole apparatus." Similar foramina are present in all known squalodont skulls. In the progressive specialization and perfection of the squalodont skull during Oligocene time, the postorbital constriction was eliminated by the exclusion of the parietal bones from the vertex and the abutting of the frontal bones against the upper border of the supraoccipital. In the course of this telescoping process the backward overthrust of the maxillaries was continued until they met a barrier wall of bone, the crest of the supraoccipital. Hence in all known squalodonts the maxillaries are in contact posteriorly with the upper border of the supraoccipital and

goids and palatines similar to *Globicephala* but less telescoped, pterygoids forming a sinus on each side in front of choanae but without external reduplication, heterodont dentition, and the symphysis of the mandible extending backward to the level of the sixth tooth counting forward from the last. Curiously enough these short beaked squalodonts appear to be restricted to the Southern Hemisphere, where they have been found in association with the more widely distributed long-beaked types. Several fairly well preserved skulls of *Prosqualodon australis* have been collected in Patagonia. An exceptionally well preserved skull of another species, *Prosqualodon davidi* was

Squalodon bariense

FIG. 6. LATERAL VIEW OF SKULL OF SQUALODON BARIENSE, MIDDLE MIOCENE, FRANCE

cover the underlying lateral extensions of the frontal bones.

Prosqualodon had 14 teeth in each upper jaw and hence the total complement of teeth would number 56, if the lower teeth, which are not known, equal the upper. The 3 incisor teeth are lodged in the premaxillary bone as in other squalodonts. Briefly stated this genus is characterized by maxillaries extending backward beyond the premaxillaries and abutting against the supraoccipital, a short broad rostrum, a deep mesorostral trough, narial passages nearly vertical, passages for olfactory nerves separated by mesethmoid, combined lachrymal and jugal wedged in between maxillary and anterior margin of supraorbital process of frontal, robust zygomatic processes, relations of pterygoids and palatines similar to *Globicephala* but less telescoped, pterygoids forming a sinus on each side in front of choanae but without external reduplication, heterodont dentition, and the symphysis of the mandible extending backward to the level of the sixth tooth counting forward from the last. Curiously enough these short beaked squalodonts appear to be restricted to the Southern Hemisphere, where they have been found in association with the more widely distributed long-beaked types. Several fairly well preserved skulls of *Prosqualodon australis* have been collected in Patagonia. An exceptionally well preserved skull of another species, *Prosqualodon davidi* was recently discovered at Wynyard, Table Cape, Tasmania.

The tendency of cetaceans descended from the same stock to diverge in character as they become specialized is well illustrated by the short-beaked and long-beaked porpoises which comprise the family Squalodontidae. Inasmuch as these squalodonts were already differentiated into at least three distinct series at the dawn of the Lower Miocene, their predecessors must have flourished in the Oligocene seas, yet the family appears to have had but one survivor in the Pliocene pelagic faunas. Very little is known in regard to the geographic distribution of the series typified by *Prosqualodon* and *Neosqualodon*, yet *Squalodon* and its relatives are known to have had a very extensive

distribution. *Prosqualodon* is the best known member of the short-beaked series. *Phoberodon* and *Squalodon* may be taken as typical representatives of the least specialized long-beaked series, while *Neosqualodon* with its elongated rostrum and excessively increased dentition undoubtedly represents the most highly specialized series.

The relations of the cranial bones in all of the long-beaked squalodonts belonging to the *Phoberodon-Squalodon* series appear to be essentially the same, and they differ from one another merely in certain minor details. The slender rostrum is nearly twice as long as the braincase. The backward thrust of the rostrum has carried the maxillary over the frontal considerably beyond the level of the orbit, and its posterior edge abuts against the supraoccipital. The frontals, which lie underneath the maxillaries, are also in contact posteriorly with the supraoccipital, and the parietals are excluded from the vertex of the skull. The mesethmoid divides the frontal fontanelle into two orifices, provides additional support for the vertex of the skull, and forms a thin veneer of bone around the dorsal and lateral faces of the presphenoid between the narial passages.

For *Phoberodon arctirostris* (Cabrera, 1926) of the Lower Miocene Patagonian marine formation of Chubut, a skull and nearly complete skeleton are known. The telescoping of the braincase and the contours of the entire skull are similar to *Squalodon*, but the zygomatic processes are much more robust. If the presence of rudimentary basal cusps on the penultimate maxillary molar and the two posterior mandibular molars has any deep seated significance, the dentition of *Phoberodon* must be considered as more primitive than that of *Squalodon*. Cabrera contends that the dental formula of *Phoberodon* should be written as follows: I. 3/3; C. 1/1; Pm. 6/6; M. 5/3 = 56. It is at least certain that this squalodont had 11 trenchant cheek teeth in each upper jaw and 9 in each lower jaw. The high and rather narrow scapula has a large broad acromion and a small coracoid process. The humerus has assumed the peculiar form of living odontocetes. The cervical vertebrae are free. The vertebral column is incomplete, but Cabrera concluded that this porpoise must have had 7 cervical, 9 dorsal, 12 lumbar, and 18 or 20 caudal vertebrae.

The genus *Squalodon* first makes its appearance in the upper division of the Lower Miocene in Italy near Belluno, where two species have been recognized. According to Dal Piaz (1916), *Squalodon bariense* with 58 teeth occurs only in the lower level of the Upper Langhian stage and the second species, *Squalodon bellunense*, with 56 teeth in the upper level. The teeth of *Squalodon* are increased above 44, the typical eutherian number, and consequently have been the subject of varying interpretations. Dal Piaz contends that 8 or 9 of the cheek teeth are premolars and that the molars may vary from 1 to 3. On the other hand, Van Beneden, Zittel, and others have interpreted the cheek teeth as comprising 4 or 5 premolars and 5 to 7 molars. Whatever may be the correct interpretation of the dental formula, the cheek teeth in the upper jaw of *Squalodon* are known to vary from 10 to 12 and in the lower jaw from 9 to 11. At least 62 teeth were present in the skull of *Squalodon zitteli* (Paquier, 1894; Zittel, 1876–77), a Middle Miocene species found in the neighborhood of the village of Bleichenbach in lower Bavaria. This squalodont had 12 cheek teeth in each upper jaw. This is especially interesting in view of Winge's suggestion (1921, p. 24) that the increase in cheek teeth above the typical number 7 might

have been produced by the intercalation of 4 milk teeth in the series, if they were found not to exceed 11. The Miocene genus *Squalodon* (Kellogg, 1923) with its telescoped and shortened braincase, limited facial depression, large temporal fossae, heterodont dentition, and elongated mandibular symphysis, is not uncommon in European and North American formations of Middle and Upper Miocene age. Their skulls measured about 3 feet in length, and according to our present knowledge these squalodonts scarcely attained a length of 16 feet.

The slender-beaked *Neosqualodon assenzae* (Dal Piaz, 1904; Gemmellaro, 1921) represents one of the odontocete extremes in the increase and elaboration of a heterodont dentition. This extinct porpoise was a member of the pelagic fauna of the upper division of the Langhian stage of the Lower Miocene and has been found at two localities in Sicily. Fortunately the left side of the skull and the left mandible found in an asphalt pit in the Tabuna region near Ragusa, province of Siracusa, Sicily, are sufficiently complete for the determination of the dental formula. It is certain that *Neosqualodon* has 3 incisors and 1 canine tooth in each jaw, and that there are 26 cheek teeth in the mandible. The skull was then furnished with something like 120 teeth. Each of the 10 posterior teeth in the mandible has one or more accessory cusps on the anterior and posterior cutting edges. Some of the lower teeth have as many as four accessory cusps on the anterior cutting edge. At least 7 of the posterior maxillary teeth are serrated on both cutting edges. The rostrum and mandible are unusually elongated, and the rostrum is fully three times as long as the braincase. The braincase, so far as known, is similar to *Squalodon* with the narial passages moved backward beyond the level of the preorbital angles of the supraorbital processes. The lachrymal and the jugal with its long styliform process are likewise similar. The skull of *Neosqualodon* measures about 21 inches in length. The subsequent history of this series is unknown.

The Miocene squalodonts seem to represent a line of development that was neither antecedent to any group of modernized porpoises nor adapted to environmental conditions of the Pliocene. A late survivor, *Prionodelphis rovereti* (Frenguelli, 1922), occurs in the estuary-facies of the Lower Pliocene Parana formation in the province of Entrerios, Argentine Republic. Judging from their shark-like teeth, these squalodonts were well adapted for a predaceous life, and hence could secure an adequate food supply wherever fish or small pelagic mammals were present in sufficient numbers to insure easy capture. Unless the prevailing pelagic conditions were radically different during the Miocene than at present, their distribution should correspond in a general way with that of the living killer whale (*Orcinus*). Remains of squalodonts have been found in Europe, North America, South America, New Zealand, and Australia.

INIIDAE

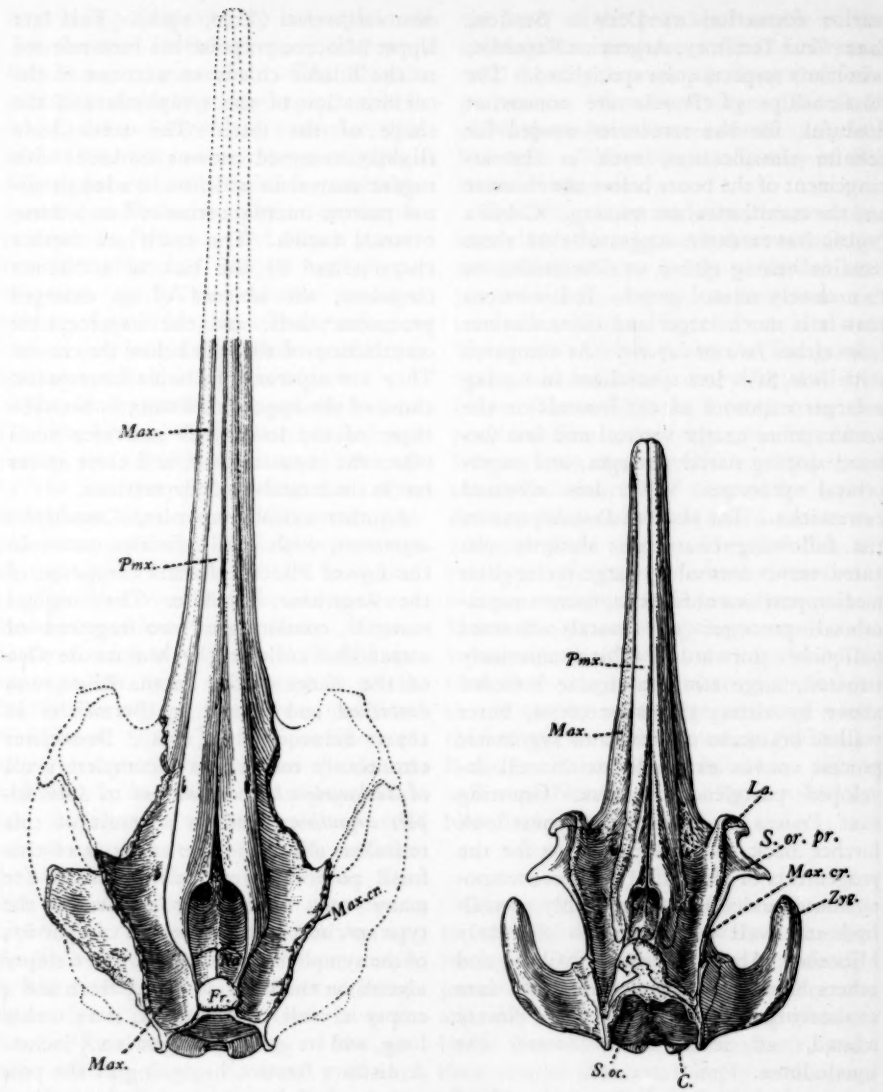
Our knowledge of the Tertiary history of the iniids is most unsatisfactory, resting as it does upon a few imperfectly preserved fragments of skulls of Miocene and early Pliocene age. The teeth of these iniids have lost their heterodonty, and their cranial characters imply as long a geological history as any of the extinct porpoises associated with them during Miocene time.

Proinia patagonica (True, 1909), which was based on an imperfect crushed skull and a single cervical vertebra obtained from the Lower Miocene Patagonian

marine formation at Darwin Station, Santa Cruz Territory, Argentine Republic, is in many respects quite specialized. The relationships of *Proinia* are somewhat doubtful, for the structures needed for definite classification, such as the arrangement of the bones below the choanae and the maxillaries, are missing. Cabrera (1926) has recently suggested that these remains belong either to *Diochotichus* or to a closely related genus. It is obvious that it is much larger and quite distinct from either *Inia* or *Lipotes*. As compared with *Inia*, it is less specialized in having a larger exposure of the frontals on the vertex, more nearly vertical and less forward sloping narial passages, and supraorbital processes with less elevated extremities. The skull of *Proinia* presents the following characters: abruptly elevated vertex formed by large rectangular median portions of frontals, narrow supraorbital processes of frontals directed obliquely forward, orbit anteriorly situated, large temporal fossae bounded above by strong ridges or crests, outer wall of braincase convex, and zygomatic process convex externally with well developed postglenoid process. Granting that *Proinia* is a true iniid we must look further back in geological time for the progenitors of this family, for contemporaneous squalodonts were highly specialized and well established in the early Miocene. Abel, Winge, Miller, and others have construed the available data as showing that the iniids, if not closely related, at least lean toward the squalodonts.

A section nearly 8 inches in length of the symphysial region of the mandibles, with six pairs of alveoli and without longitudinal external furrow, which was found associated with four loose teeth in the upper San Pablo formation near Rodeo, California, formed the basis for *Hesperocetus californicus* (True, 1912). This late Upper Miocene porpoise has been referred to the Iniidae chiefly on account of the conformation of the symphysis and the shape of the teeth. The teeth have slightly recurved crowns covered with rugose enamel in addition to a longitudinal postero-internal carina and an antero-external carina. The teeth are further characterized by the lack of a distinct cingulum, the absence of an enlarged protocone shelf, and the imperceptible constriction of the root below the crown. They are separated by wide interspaces, those of the upper jaw fitting in between those of the lower jaw and vice versa when the jaws are shut, and their apices rest in the interalveolar depressions.

Another extinct porpoise, *Saurodelphis argentinus*, with iniid affinities occurs in the Lower Pliocene Parana formation of the Argentine Republic. The original material, consisting of two fragments of a mandible collected by Montes de Oca on the shore of the Parana River, was described and figured by Burmeister in 1871. Subsequently (1891), Burmeister erroneously referred an incomplete skull of *Ischyrorhynchus vanbenedeni* to *Saurodelphis argentinus*, and as a result of this mistaken allocation the affinities of this fossil porpoise were misinterpreted for many years. The larger fragment of the type specimen, which consists of a portion of the symphysis with 6 teeth and 6 empty alveoli on the left side, and 3 teeth and 4 empty alveoli on the right, is 15 inches long, and its greatest height is 2.5 inches. A distinct furrow, beginning at the posterior end of the symphysis and extending forward to near the extremity, traverses the lower border of the external face. The alveoli are elliptical, and behind and anterior to each is a small circular depression placed outside of the alveoli instead of in line with them, apparently



Ischyrorhynchus vanbenedeni *Inia geoffrensis*

FIG. 7. DORSAL VIEWS OF SKULLS

Ischyrorhynchus vanbenedeni, Lower Pliocene, Parana, Argentine Republic. *Inia geoffrensis*, Santarem, Brazil

marking the position of the apices of the upper teeth when the jaws are shut. The teeth are large, compressed, and not closely approximated, with acute conical crowns covered with rugose enamel. Between the base of the crown and the

neck of the root is a well marked cingulum. The root is gibbous below the neck. Some of the teeth have the extremity of the root irregularly divided into three branches. The smaller teeth resemble the anterior teeth of the living South American genus *Inia* in the shape of the crown, the cingulum, and the compression of the distally expanded root. None of these teeth exhibit the distinct internal protocone shelf that is so characteristic of the crown of posterior teeth of *Inia*.

In 1891, Burmeister described and figured an imperfect skull collected by Artemio Carreras at La Curtiembre, near Parana, Argentine Republic. In restoring this skull, Burmeister used the living *Stenodelphis* as a model and added the end of the rostrum of another porpoise. This composite specimen was erroneously referred to *Saurodelphis argentinus*, as has already been pointed out by Abel (1909) and Rovereto (1915). Burmeister was the first to suspect that this extinct porpoise might be identical with *Ischyrorhynchus vanbenedeni*, but it remained for Cabrera (1926) to allocate the skull to that genus and species. This strongly telescoped Lower Pliocene porpoise skull differs from all known iniid skulls in having the zygomatic processes placed far forward, and the maxillaries are pushed farther back toward the occiput. The outer borders of the maxillaries in the supraorbital and supratemporal regions are strongly bent upward, recalling *Platanista* in some respects. Doubtless a certain resemblance exists between *Ischyrorhynchus*, *Inia*, and *Platanista*, but not a close one. It is obvious that the lateral crests of the maxillaries were much higher than in *Inia*, and it is possible that when complete they may have resembled those of *Platanista*. The inclination of the posterior wall of the narial passages is much less steep than in either *Inia* or *Platanista*, and the small, conspicuously elevated vertex is formed by the frontals. Although both nasal bones are missing, the cavities in which they were lodged are distinct enough to determine their proportions, and it is fairly certain that they were pressed against the frontals on the posterior wall of the narial passages. The irregularly spaced teeth are large, elliptical in section; the crowns of the teeth are conical and low, with apex slightly recurved backward, and covered with rugose enamel. The roots of the teeth are thickened, and the anterior teeth are strongly inclined forward. The imperfect skull, which lacks the end of the rostrum, has a length of about 25 inches and was nearly 13 inches in breadth across the zygomatic processes when complete, while a large complete skull of *Inia* has a length of but 21 inches and a zygomatic breadth of 9¼ inches.

Skulls of living river porpoises of the family Iniidae differ from all other odontocetes in having a more or less fenestrated, freely projecting, fortuituous process of the maxillary, extending backward outside of the sinus in front of the choana to or beyond the level of the sphenoid fissure. The South American *Bouto* (*Inia geoffrensis*) and the Chinese *Peh Ch'i* (*Lipotes vexillifer*), now living in Tung Ting lake and its tributaries, are porpoises of small or moderate size whose skulls have elongated rostra; narrow facial depression with external borders of maxillaries bent upward; maxillaries extending forward to extremity of rostrum; orbits situated in front of level of narial passages; nasals flattened up against frontals on anterior wall of braincase, contributing upper border of posterior wall of narial passages and overspread inferiorly by mesethmoid; elevated vertex; elongated zygomatic processes; palatine forming part of anterior wall of narial passage and separated

from its mate on median line of palate by axial ridge of vomer; simple pterygoids neither spreading laterally over alisphenoid nor reduplicated along either margin, and not completely covering palatines on ventral aspect of skull; long mandibular symphysis; and numerous teeth in both jaws, but those in the upper jaw lodged solely in the maxillaries. The crowns of the teeth are covered with nodular or reticulate enamel and are anteroposteriorly compressed; the roots are laterally compressed and expanded distally. The teeth of *Inia* have a large internal protocone shelf covered with rugose enamel, while those of *Lipotes* have this portion of the tooth very much reduced. The cervical vertebrae are all free.

ZIPHIIDAE

In addition to the squalodonts there occurs in the Lower Miocene Patagonian formation a peculiar extinct porpoise *Diochotichus vanbenedeni*, which possesses so many anomalous features that its relationships were somewhat of a puzzle for many years. Moreno (1892), the original describer, did not reach any conclusion as to its family position. Lydekker (1894) considered it to be a primitive platanistid, and True (1910) thought that it was a squalodont with simple, single-rooted, conical teeth. Dal Piaz (1916) made a new family, Squalodelphidae, for the reception of this porpoise and an allied cetacean, *Squalodelphis fabianii*, found in the Upper Langhian stage of Belluno, Italy. More recently Winge (1918, 1921) and Cabrera (1926) have considered *Diochotichus* to be the most primitive known form of the beaked whales (family Ziphiidae). Four more or less complete skulls of this peculiar ziphioid whale have been collected in Chubut and Santa Cruz Territories, Argentine Republic.

The skull of *Diochotichus* is characterized as follows: 23 teeth in each maxillary and 19 in each mandible; posterior teeth are short, with single main cusp, covered with smooth enamel, and have an anterior and posterior minute tubercle; anterior teeth are conical, long, and curved; all the teeth are single rooted; premaxillary expanded anteriorly and not touching posteriorly upon the frontal; maxillary bent upward behind premaxillaries, with its inner margin on a level with the vertex and in contact posteriorly with crest of supraoccipital; nasal bones large, not overhanging narial passages; large olfactory foramina separated mesially by mesethmoid; low broad supraoccipital; backward extension of posterior margin of temporal fossa; zygomatic processes large, thick, oblong, and very little divergent; elongate sinus on ventral surface of maxillary anterior to choana; pterygoid with an inner vertical plate and an outer more or less horizontal plate, which conceals the alisphenoid; mandibular symphysis long; mandible strongly convex posteriorly; and length of skull 23 to 25 inches. The facial depression is farther forward than in living ziphioids, but is clearly antecedent to the postrostral depression seen on skulls of living beaked whales, while the elevation of the vertex is what might be expected in a precursor of the more highly specialized types of the later Miocene. The cervical vertebrae are free, and as True pointed out the characters exhibited by the vertebral column are distinctly ziphioid.

It shares with *Squalodon* the following important characters: orbital plates of maxillaries do not completely cover the supraorbital processes of the frontals; vomerine trough wide; zygomatic processes large, thick, and oblong; long mesethmoid separating the olfactory foramina; and premaxillaries expanded anteriorly

FIG. 8. DORSAL VIEWS OF SKULLS

Diochotichus vanbenedeni, Lower Miocene, Patagonia. *Mioziphius belgicus*, Upper Miocene, Belgium. *Chonziphius planirostris*, Upper Miocene, Belgium. *Ziphius cavirostris*, Newport, Rhode Island.

and abbreviated posteriorly. The relations of the bones on the ventral surface of the skull are quite different from conditions in the iniids.

Squalodelphis differs from *Diochotichus* in the following particulars: antorbital maxillary protuberance slightly more accentuated; rostrum narrower at base; maxillary almost wholly concealed at base of rostrum by overlying premaxillary; 15 teeth in each maxillary and mandible; posterior teeth unicuspid, compressed, bicarinate, and acuminate, and covered with rugose enamel with a cingulum formed by rugosities on internal side at base; length of skull about 25 inches; symphysis one half total length of mandible.

A distinctly modernized ziphioid, *Mioziphius belgicus* (Abel, 1905), which is not so distantly related to living beaked whales, was a member of the Upper Miocene pelagic fauna of the Belgian coast. Its skull is slightly larger than that of the living *Mesoplodon*. It is rather ponderous and slightly asymmetrical. It has the thick extremities of the premaxillary bones bent upward opposite the nasal bones; the olfactory foramina are open even in old individuals; large prenarial fossa; no mesorostral ossification; maxillaries strongly swollen in front of antorbital notches; premaxillaries in contact on distal half of rostrum, completely concealing vomerine trough; maxillary with 37 to 48 closely approximated alveoli, but with intervening septa almost entirely obliterated, giving rise to a broad shallow alveolar gutter. The mandibles have a short symphysis, about one-fourth the length of the rostrum, and are furnished with two pairs of large functional teeth, of which the anterior or terminal pair is the larger. These teeth are lodged in projecting sockets formed of cancellous bony tissue. The mandibular dentary groove is narrow, shallow, and reduced posteriorly. With the exception of the two pairs of mandibular teeth, the others, if present, were lodged in the gum.

The ziphioid genera *Mioziphius*, *Choneziphius*, and *Ziphius* are a direct outcome of a peculiar arrangement of the bones that enter into the composition of the vertex of the cranium. We have seen that the vertex was somewhat raised in the Lower Miocene genera *Diochotichus* and *Squalodelphis*, and that the premaxillaries were blocked off posteriorly by the raised crest-like postero-internal margins of the maxillaries. Any additional backward thrust of the maxillaries and premaxillaries would elevate the posterior extremities of these bones, for the maxillaries were in contact with the crest of the supraoccipital in these Lower Miocene ziphioids. Partly in this manner and partly by actual bony outgrowths, the skulls of these Upper Miocene ziphioids acquired their peculiar elevated vertex overhanging a large bowl-shaped postrostral depression.

The skull of *Choneziphius planirostris* (Cuvier, 1836; Capellini, 1885; Weber, 1917) is somewhat unusual in that it is the only Upper Miocene ziphioid known to have a premaxillary that retains distinct vestiges of alveoli, notwithstanding the probability that if teeth were present in the upper jaw they were lodged in the gum. This extinct ziphioid, or closely related species, occurs in the Upper Miocene sands of the Antwerp Basin, the Edisto marl of South Carolina, the Pliocene Red Crag of Suffolk, England, and the Pliocene sands near Siena, Italy. This ziphioid skull is distinguished by having an attenuated rostrum not noticeably widened at the base, but somewhat swollen and thickened near the middle; form of rostrum subject to age, individual, and perhaps sexual variations; prenarial

fossa formed by the ankylosed premaxillaries, which develop an oblique sinistral crest along their line of contact, dividing the fossa into a large right cavity and a smaller left cavity; premaxillaries either closely approximated on the median line anterior to prenarial fossa or completely fused in old individuals; although concealed from view the narrow vomerine canal remains open; maxillaries not developing antorbital tuberosities; antorbital notch double; olfactory foramina large; mesethmoid thoroughly ossified; posterior extremities of premaxillaries bent upward behind the narial passages, forming the lateral borders of the high vertex; nasal bones reduced and lodged in deep fossae, which encroach upon premaxillary crests; lachrymal fused with frontal, maxillary, and jugal; maxillary and premaxillary with narrow alveolar gutter; vestigial septa between alveoli not visible on many specimens; length of skull in two old individuals about 27½ inches when complete.

Inasmuch as there are ten recognized living species of the genus *Mesoplodon*, there can be no objection to the assumption that species of these ziphioids were equally if not more numerous in preceding geological periods. Remains of extinct species of *Mesoplodon* are rather common in the Upper Miocene sands of the Antwerp Basin (Abel, 1905), the Edisto marl of South Carolina (Leidy, 1877), the Red Crag of Suffolk, England (Owen, 1870), and the Pliocene deposits of Italy (Vigliarolo, 1894). Unfortunately the majority of the fossil specimens referred to this genus consist solely of rostra, which are subject to age, individual, and sexual variations. Some of these specimens differ very little from living species, and one of them, *Mesoplodon longirostris* (Cuvier, 1836) may have been a precursor of the living beaked whales, *Mesoplodon bidens* and *M. europaeus*.

The palaeontological evidence bearing on the ancestry of the ziphioids indicates that they were derived from ancestors with functional teeth in both jaws. In the course of geological history the maxillary teeth have been suppressed except for the not infrequent occurrence of vestigial teeth buried in the gums, the symphysis of the mandible has been shortened, and the mandibular teeth have been reduced to one or two pairs. One of the distinctive features of living ziphioid whales is the presence of distinct jugal and lachrymal bones. The normal mammalian relationships of the jugal and lachrymal are transposed, for the former comes to lie in front of the latter on the ventral aspect of the skull. Living ziphioids retain a remnant of the dentary groove, which in some species consists of a longitudinal basirostral groove beginning in a blind pit below the antorbital maxillary tuberosity and extending forward along the side of the rostrum. As many as 17 to 19 vestigial maxillary teeth have been found in the gums of *Mesoplodon grayi* (Oliver, 1922). The antorbital maxillary tuberosities become by further enlargement the enormous longitudinal crests of *Hyperoodon rostratus* (Harmer, 1924). The rostrum has been deepened and solidified by ossification of the mesorostral cartilage. Some of the remarkable alterations that take place in the ossification of the rostrum during growth have been described by Forbes (1893). All of the living ziphioids (True, 1910) exhibit the same peculiar twisting, forward curling, and elevation of the posterior extremities of the premaxillaries and the maxillaries. The freely projecting nasal bones come to overhang the narial passages. The median portion of the supraoccipital bone has been raised higher to conform to the unusual elevation of the vertex. Another peculiarity is that the grooved anterior process of the periotic is lodged in a

slender ventrally directed dactyloid process of the squamosal. The unusual size of the air-sac at the outer side of the pterygoid, which is shaped to fit it, is another peculiarity of modernized ziphioid skulls. The base of the pterygoid has spread laterally, covering or nearly covering the alisphenoid bone, but the external reduplication is reduced to a low ridge. The cervical vertebrae tend to ankylose with one another. The dorsal, lumbar, and caudal vertebrae have high neural spines for the huge muscle masses associated with the caudal flukes. The wrist and finger bones are relatively small.

It would appear that the Lower Miocene ziphioids stand nearer to the squalodonts than to the sperm whales. In the past the beaked whales have been regarded as near relatives of the physeteroids, a conception which is disputed by Miller (1923), who calls attention to important morphological differences, such as the relation of the pterygoids to the palatines, and the structural features of the vertex.

DELPHINIDAE

The obliteration of the postorbital constriction by the exclusion of the parietals from the vertex and the accompanying contact of the supraoccipital with the frontals was brought about by a crushing together of the anterior and posterior elements of the skull. This stage of telescoping was fully established in the odontocetes of the Lower Miocene.

Scarcely less interesting than the foregoing is the fact that the maxillary had already reached its extreme posterior extension in the squalodonts *Phoberodon* and *Prosqualodon*, the ziphioid *Diochotichus*, and the delphinoid *Argyrocetus*. In all of these Lower Miocene South American porpoises the orbital cavity and the temporal fossa are roofed over by two flattened plates of bone, the uppermost being the maxillary and the lowermost the lateral extension of the frontal. The temporal fossa has not suffered any marked reduction because of any actual increase in size of the braincase. In only one of the preceding genera, *Diochotichus*, do the nasal bones retain a trace of their earlier function of providing a roof for the nasal cavity. What is of greatest interest, however, is the entire absence of any indication of heterodonty in these ziphioid and delphinoid types, and the fact that the premaxillaries project anteriorly beyond the maxillaries in all of these extinct porpoises. All of these genera, without exception, show that the narial passages have been forced backward against the anterior wall of the braincase and that their inclination is determined by the contour of this surface.

According to Miller (1923) the family Delphinidae comprises five distinct subfamilies, which he designated as follows: Delphininae, Eurhinodelphininae, Stenodelphininae, Delphinapterinae, and Monodontinae. The validity of the subfamily Eurhinodelphininae is somewhat doubtful, for it includes extinct porpoises in which the premaxillary is said to have been lengthened so that it projects conspicuously in front of the maxillary for a distance equivalent to one-fifth of the total, a condition that is not apparent in American specimens determined as *Eurhinodelphis*. The long beaked Lower Miocene porpoise *Argyrocetus* has been referred to this group by Cabrera (1926). As a general rule among more recent delphinoids the extreme tip of the premaxillary tends to lose its position on the ventral face of the rostrum because of the forward extension of the underlying maxillaries, and the teeth which were originally implanted in it are lost. A wide variety of extinct and living porpoises (True, 1889) are included in the

family Delphininae, ranging in antiquity from the Lower Miocene to the present time. Extinct relatives of the Stenodelphininae are not known with certainty earlier than the Lower Pliocene. The subfamilies Delphinapterinae and Monodontinae have a shorter geological history, the occurrences being restricted to the Pleistocene. One of the most remarkable features of the odontocete skull is its plasticity, which not only permitted a reshaping of its contours in conformity with environmental conditions imposed upon it, but also in some instances seemingly followed capricious paths of development. The rostrum may be either lengthened as in *Cyrtodelphis* or broadened as in *Globicephala*, but it is never deepened or solidified in the delphinoids.

Porpoises with long slender rostra predominated in the pelagic faunas of the Lower Miocene, as is evidenced by the occurrence of *Argyrocetus* in Patagonia, and *Ziphiodelphis*, *Cyrtodelphis*, *Eoplatanista*, and *Acrodelphis* in Italy. The occurrence of one little known, supposedly rather short-beaked porpoise, *Protodelphinus*, near Belluno was mentioned by Dal Piaz in 1922. The skeleton of another short-beaked porpoise, *Delphinavus newhalli* (Lull, 1914), measuring about 5 feet in length, has been found in the Lower Miocene Vaqueros formation of San Luis Obispo County, California. The skull is eleven and a half inches long, three-fifths of which is taken up by the rostrum. The mandibular symphysis is relatively very short, equivalent to slightly more than one-eighth of the total length of either ramus. It is interesting to note that the premaxillary bone is toothless and that the total complement of teeth is considerably increased above the normal, there being at least 180 teeth present. The teeth are all alike, with slightly recurved conical crowns covered with smooth polished enamel and no indication of carinae. The cervical vertebrae are separate, and there are at least 12 rib-bearing vertebrae. The fore limb or pectoral flipper is essentially delphinoid, with modified carpal bones and the usual arrangement of the metacarpals and phalanges in the digits. From some such type of extinct porpoise as this have descended the living porpoises *Delphinus* and *Prodelphinus*. In attempting to follow out this subject of the late Tertiary history of the delphinoids many equally interesting types of extinct porpoises must be omitted, and the interested reader is referred to the bibliography for references to these species.

As with many other groups of extinct mammals, we have an imperfect knowledge of the earlier Tertiary history of the long-snouted porpoises, which had already reached the fulness of their development in the Lower Miocene. They were then associated with several types of undoubtedly carnivorous squalodonts, but outlived most of them to find companions in the even longer-snouted extinct porpoises of the Upper Miocene. Whatever their previous geological history may have been, we are confronted in the Lower Miocene with a highly telescoped delphinoid type of skull, in which the backward overthrust of the maxillary was stopped by the crest of the supraoccipital and the rostrum conspicuously elongated. The splitting up of these long-snouted porpoises into several series had already commenced in the Lower Miocene, and each of these phyla, as we shall presently see, followed from then on their own peculiar path of development. A brief history of three of these series follows.

The first to be considered is taken to include the Lower Langhian *Argyrocetus*, the Upper Langhian *Ziphiodelphis*, and the Middle and Upper Miocene *Eurhinodelphis*.

This series includes porpoises with very long rostra, whose distal extremities are edentulous, or if teeth were present they were implanted in a dentary ligament along the vestigial alveolar groove. A somewhat damaged skull, nearly complete mandibles, including most of the symphysis, four cervical vertebrae and

tion has been eliminated and the backward rostral thrust has carried the maxillary to the supraoccipital. The full complement of teeth exceeds 200. The vertex is limited to a narrow strip of the conjoined frontals, into the anterior borders of which the squared nasal bones have sunk. Cabrera (1926) has pointed out the great

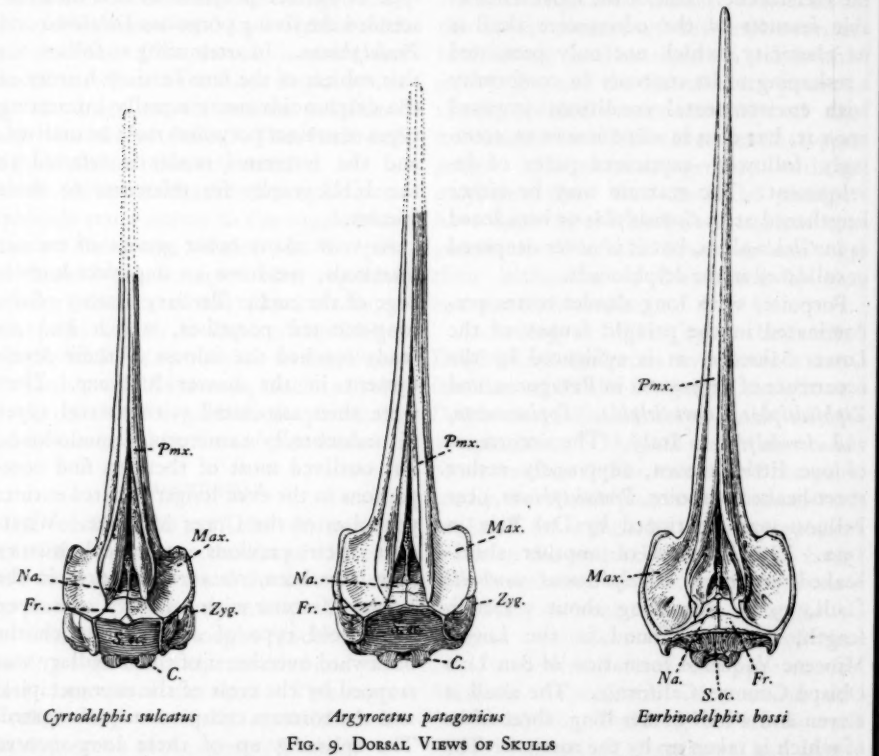


FIG. 9. DORSAL VIEWS OF SKULLS

Cyrtodelphis sulcatus, Lower Miocene, Italy. *Argyrocetus patagonicus*, Lower Miocene, Patagonia. *Eurhinodelphis bossi*, Middle Miocene, Maryland.

one dorsal found in the Patagonian marine formation at Castillo, opposite Trelew, Chubut Territory, formed the basis for *Argyrocetus patagonicus* (Lydekker, 1894). This slender-beaked skull shows how widely these early Miocene porpoises have departed from the known Eocene odontocetes, for the postorbital constriction has been eliminated and the backward rostral thrust has carried the maxillary to the supraoccipital. The full complement of teeth exceeds 200. The vertex is limited to a narrow strip of the conjoined frontals, into the anterior borders of which the squared nasal bones have sunk. Cabrera (1926) has pointed out the great length of the premaxillaries as compared with the maxillaries, and has estimated that the former exceed the latter by an interval equivalent to one-fifth of the total length of the skull. The mandible when complete measured about 35 inches in length, of which fully three-fifths was taken up by the symphysis. Some-

thing like 50 teeth were implanted in each ramus, and ten of them were situated behind the symphysis. The latter ends in an upwardly directed and edentulous spatulate-like tip.

Further evidence that the teeth of this series of extinct porpoises were in the process of reduction is afforded by *Ziphiodelphis abeli* (Dal Piaz, 1908, 1922), whose skull and mandibles were found in the sand pits of Bolzano, Italy. Although the extremity of the rostrum is missing, this skull measures more than 30 inches in length. The anterior teeth were very much reduced in size, but the posterior maxillary teeth were functional and lodged in distinct alveoli. The alveoli disappear near the anterior end of the rostrum and merge with the alveolar groove, which indicates that the teeth near the extremity must have been held in place by a dental ligament. Unfortunately the crowns of most of the teeth are so worn that their characters are obliterated, but the few that are complete have the crowns covered with smooth enamel without basal rugosities. The mandibular symphysis is long, and the posterior angle is similar to *Eurhinodelphis*.

The lower jaws of *Eurhinodelphis bossi* (Kellogg, 1925) from the Calvert formation of Maryland are not as long as the rostrum, and the terminal portions of both jaws have no alveoli and apparently lacked teeth. In some species of this genus, as for instance *Eurhinodelphis longirostris* (Abel, 1902, 1905), the rostrum is excessively elongated, occupying nine-elevenths of the total length of the skull. Each maxilla is furnished with approximately 60 alveoli, in front of which is a narrow alveolar groove. The symphysis is slightly longer than the free portion of either mandibular ramus. Olfactory foramina are present in some species, but in others these passages are closed by the overspreading ethmoids. The nasal bones are small, and the frontals are contracted at the vertex, forming a narrow exposed strip, but sometimes are entirely covered by the supraoccipital. The lachrymal bone is either separated from the jugal by suture or ankylosed with it. The closely approximated teeth show a progressively slight increase in height and thickness posteriorly. The crowns of these teeth are slightly recurved, anteroposteriorly compressed, and covered with smooth enamel. The roots are quite variable in shape, some attentuated and others expanded distally. Judging from the number of distinct alveoli, the skull and mandibles were furnished with 220 teeth in addition to whatever number may have been present in the alveolar grooves. A reasonable estimate based on the length of the skull and the proportions of the 7 cervical, 10 or 11 dorsal, 11 lumbars, and 19 caudal vertebrae gives a total length of approximately 15 feet for this extinct porpoise. The cervical vertebrae are not ankylosed. The fore limb is similar to those of living delphinoids. The bones of this extinct porpoise are now known from Europe, North America, and Japan, in formations not later than the Upper Miocene. As to the cause of their final extinction we have no evidence other than that they had probably become so fixed and unplastic in their structure and habits that they were unable to keep pace with their associates. Toward the close of their history they become fairly numerous and seem to have been one of the dominant porpoises of the Upper Miocene.

The second series includes *Cyrtodelphis sulcatus*, a long-beaked porpoise with a very specialized and peculiar dentition, which begins its career in the Langhian stage of Europe, specimens having been

found in the coarse green quartz sands at Eggenburg, north of Vienna, Austria (Abel, 1899), in the sand pits near Belluno, Italy (Dal Piaz, 1901, 1903, and 1905), and the Uadi Faregh of Egypt (Stromer, 1905). The anterior teeth in both jaws are elongated, with pointed, lanciform, and laterally-compressed smooth-enameled crowns, the anterior and posterior edges being trenchant. These single-rooted teeth are firmly implanted in distinct alveoli, and the laterally compressed roots are abruptly expanded below the crown, forming a blade, which in some teeth is directed almost at right angles to the perpendicular axis of the crown. Posteriorly the teeth little by little diminish in height. The inwardly curved crowns become more conical with minute tubercles on inner side at base, and the roots less compressed and often thickened below the crown. The implantation of the teeth is oblique, and there were something like 50 teeth on each side in each jaw. The elongated rostrum is at least equivalent to three-fourths of the total length of the skull. The skull is further characterized by a rather flat vertex with relatively large exposure of the frontals, a small rhomboidal interparietal, and small antero-posteriorly compressed nasals; a low supraoccipital; rostrum with closely approximated premaxillaries, ankylosed together distally with age, and tapering less abruptly than the maxillaries; and olfactory foramina are present. The dorso-ventrally compressed and solidified symphysis is equivalent to two-thirds of the total length of the mandible, with a longitudinal ventral furrow on each side into which vascular foramina open. The skeleton is known to contain 7 separate cervical and 10 dorsal vertebrae.

The Lower Miocene porpoise *Cyrtodelphis* offers some points of unusual interest. Its skull was not only telescoped to a high degree, but also its complement of teeth has increased four or five fold above the normal eutherian dentition. *Cyrtodelphis* proved sufficiently adaptable to environmental conditions to leave descendants in succeeding pelagic faunas, and its several species have been found in the Helvetian stage of France, the Tortonian Calvert formation of Maryland (True, 1908), the Sarmatian of Heiligenstadt near Vienna (Abel, 1899), the Anversian of Antwerp, Belgium (Abel, 1905), and the supposedly more recent Bone Valley formation of Florida (Allen, 1921).

Another equally interesting porpoise from the Libano sand pit near Belluno has recently been described by Dal Piaz (1916) as *Eoplatanista italica*. The distinguished Italian palaeontologist considered this extinct porpoise to be a precursor of the living *Platanista* and cited the peculiarities of the teeth to support his contention. Without attempting to go into an extensive discussion of *Eoplatanista italica* and follow out each structural detail, it may be said that one can not well avoid being cognizant of the resemblance of this skull to the contemporary *Cyrtodelphis*. Similarity of structure, such as observed in these two extinct porpoises, can hardly be considered superficial. In so far as the cranium is concerned, *Eoplatanista* differs from *Cyrtodelphis* in having the vertex noticeably contracted in an antero-posterior direction and a reduced number of teeth, there being 40 teeth in each upper jaw and 38 in each lower jaw. Otherwise the contours and structural peculiarities of the skulls of these two porpoises are practically identical. The same observation holds true for the periotic bones. That the type skull of *Eoplatanista* belongs to an old individual is shown by the well worn teeth, which are ground down to or below the level of the base of the crown.

Changes in the shape of the root, such as may be observed when *Eoplatanista* is contrasted with *Cyrtodelphis*, are comparable to those in the teeth of very old individuals and mature specimens of the living *Platanista*. At any event the differences observed in the teeth are hardly of sufficient importance to warrant a family distinction between these two extinct porpoises. The skull of *Eoplatanista* measured about 26 inches in length and is thus a few inches shorter than that of *Cyrtodelphis*. Its relationships appear to be with *Cyrtodelphis*, and it is here considered to be a member of that series.

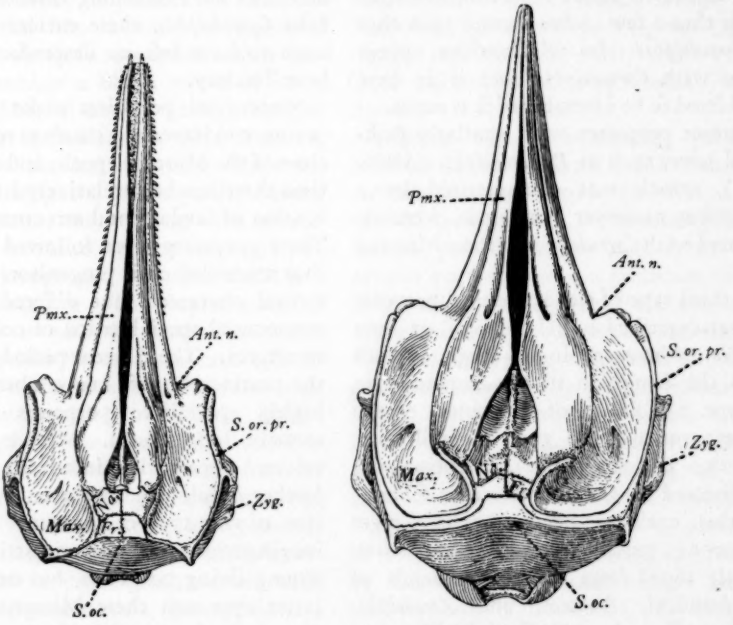
Extinct porpoises with similarly fashioned jaws, such as *Pomatodelphis* (Allen, 1921), which was characterized by a somewhat narrower symphysis, were associated with *Cyrtodelphis* in these Miocene seas.

A third type of slender-beaked porpoise is that described by Abel (1899) as *Acrodelphis*, whose geologic range extends from the Langhian to the Sarmatian in Europe. As it is not the object of the present summary to give a detailed description of each species, attention will be directed to the characteristic features of this extinct porpoise. The Lower Miocene species, *Acrodelphis krahuletzi* (Abel, 1899) from the Mugel-sands of Gauderndorf, Austria, and *Acrodelphis ombonii* (Longhi, 1898) from Libano, Italy, show that this porpoise had acquired a long narrow mandibular symphysis with acute posterior angle and a large number of closely approximated single-rooted teeth. The chief point of interest in this group of somewhat smaller slender-beaked porpoises is the pseudoheterodont appearance of the teeth. The anterior teeth have a long slender crown in contrast to the shorter, blunter, and more incurved conical crowns of the posterior teeth, which are further characterized by the presence of small accessory tubercles, conspicuous basal rugosities, and a crenelated cutting edge. The stage of telescoping is similar to that of *Cyrtodelphis*, but the vertex is smaller and more convex, the frontals are restricted to a narrow strip on the vertex, and the nasal bones are relatively larger. Another closely related porpoise, *Champsodelphis*, was associated with it in the pelagic faunas of the succeeding Miocene stages. Like *Cyrtodelphis*, these extinct porpoises seem to have left no descendants in the later Tertiary.

Modernized porpoises make their appearance in increasing numbers toward the close of the Miocene epoch, and since that time there has been relatively little modification of fundamental structural details. These porpoises were followed by types that resembled their progenitors in fundamental characters but differed in more pronounced specialization of one or more structures. The Pliocene period witnessed the extinction of many aberrant and highly specialized porpoises with extremely long rostra. Mechanical difficulties apparently interfered with a further development or even a continuation of this type of rostrum. There are brevirostrine and longirostrine types among living porpoises, but none of the latter approach these Miocene types in the relative length of the rostrum.

During the time of accumulation of the Calvert formation in Maryland, several types of short-snouted porpoises, in association with some of the more highly specialized long-snouted porpoises mentioned on the preceding pages, were frequenting the estuary which covered that area. Two of these porpoises are represented in collections by nearly complete skeletons, but the others unfortunately are still imperfectly known. When one studies the skulls of these extinct

porpoises, the conclusion can not be avoided that they represent stages through which some of those now living have passed. The Calvert porpoises, *Delphinodon dividum* (True, 1912) and *Kentriodon pernix* (Kellogg, 1927), resemble some of the smaller living porpoises rather closely, and it is not unlikely that they were as active and as graceful as any of the living types.



Kentriodon pernix *Delphinodon dividum*

FIG. 10. DORSAL VIEWS OF SKULLS
Kentriodon pernix, Middle Miocene, Maryland. *Delphinodon dividum*, Middle Miocene, Maryland

There is a marked resemblance between the extinct Miocene *Kentriodon pernix* and the living southern porpoise *Sotalia tucuxi*. The skeleton of *Kentriodon* is approximately 5½ feet long. Its telescoped skull has a short and narrow braincase, a slender rostrum, a small, more or less pentagonal vertex, the posterior extremity of the maxillary in contact with the transverse crest of the supraoccipital, extremity of rostrum formed by the premaxillaries and at least three teeth implanted in each of these bones, 40 teeth in each upper jaw and 38 in each mandible. The crowns of the teeth are recurved, with relatively smooth enamel, but with neither carinae nor accessory cusps; the roots are slender, slightly enlarged below the crown, and have a small pulp cavity.

Sotalia on the other hand lacks the tusk-like teeth at the extremity of the jaws; no teeth are implanted in the premaxillary, for it does not project beyond the maxillary; the braincase is more expanded; and the maxillary has receded from the crest of the supraoccipital.

As compared with *Kentriodon*, the skull of *Delphinodon dividum* has a large, broad

braincase, almost equal to the length of the rostrum; a strongly attentuated rostrum, whose extremity is formed by the premaxillaries, 27 teeth in each upper jaw, and 26 in each mandible. The crowns of the teeth are recurved, with rugose enamel, and distinct carinae on anterior and posterior cutting edges; posterior teeth with one or more accessory cusps; the roots are slender, gibbous below the crown, and have a large pulp cavity. The skeleton is a few inches longer than that of *Kentriodon*. The living porpoise *Cephalorhynchus* may have descended from some such type as *Delphinodon*.

There were other species of Upper Miocene porpoises whose skulls were undergoing a process of remodeling leading up to the extremely short-snouted living porpoises, such as *Neomeris*, *Phocaena*, and *Phocoenoides*. An enlargement of the braincase caused the posterior cranial elements to swell outward. Earlier porpoises have the occipital region more or less flattened in contrast to the decidedly bulging appearance of the hinder cranial region of most living delphinoids. This tendency toward enlarging the braincase resulted in further changes in the relations of certain bones. The facial region becomes broader and the tendency toward shortening and broadening the rostrum becomes more noticeable in some forms than in others. This is particularly true of the section of the delphinoids to which the living "blackfish," *Globicephala*, belongs. Porpoises with moderately long beaks are in the minority, in so far as genera are concerned, in the existing pelagic faunas.

Short-snouted porpoises, with skulls that resemble those of *Tursiops* and *Delphinapterus*, have been found at a number of localities of Pliocene age in Italy. The relations of the pterygoid and alisphenoid bones are the critical structural features that distinguish these two genera, and it is unfortunate that these details have not been ascertained. These Pliocene porpoises had not more than 66 teeth, while the living bottlenose porpoise, *Tursiops*, has a hundred or more. The trend of development in later Tertiary involves a secondary reduction of the quadrupled or quintupled dentition, and there is no evidence to indicate that recent porpoises are reversing their evolution again by undergoing an increase in the number of teeth. It is more likely that these Pliocene porpoises represent another line of development and that their descendants had the teeth further reduced. It is still uncertain whether or not the living white whale, *Delphinapterus*, which has a total of 36 teeth, is related to any of these Pliocene porpoises.

The Lower Pliocene or Plaisancian stage of Italy has at least three species of extinct porpoises that have been referred to *Tursiops*. Of these the nearly complete skeleton of *Tursiops cortesii* (Fischer, 1829; Cuvier, 1836, pl. 224, Figs. 1–2) found south of Fiorenzuola, Italy, is probably the most interesting. This has a skull with 14 teeth in each upper jaw and 14 in each mandible. Coming to the Middle Pliocene or Astian stage, we find a larger number of occurrences of extinct porpoises referred to *Tursiops*. A remarkably well preserved skull and skeleton of *Tursiops capellini* (Sacco, 1893) found near Cortazzone in the Territory of Camerano-Carasco, Italy, has 16 teeth in each upper jaw and 15 in each mandible. In both of the skeletons just mentioned the atlas and axis are fused together.

In the late Pliocene or Sicilian stage another species, *Tursiops osennae* (Simonelli, 1911) makes its appearance. This extinct porpoise has 21 teeth in the upper jaw and probably an equal number in the mandible. It was found in a

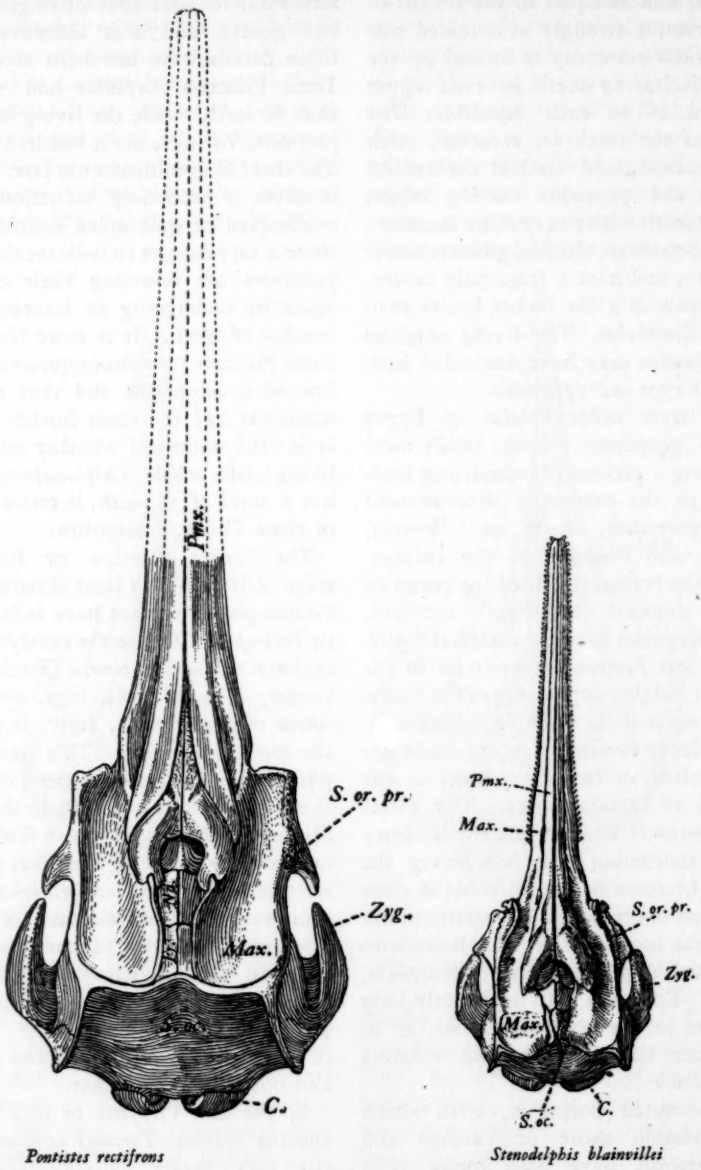


FIG. 11. DORSAL VIEWS OF SKULLS

Pontistes rectifrons, Lower Pliocene, Parana, Argentine Republic. *Stenodelphis blainvillei*, Mar de la Plata, Argentine Republic.

glauconiferous clay in the province of Siena, Italy, and seems to be a true *Tursiops*.

The living killer whale, *Orcinus orca*, seems to have descended from the same stock as *Tursiops*, and it is not unlikely that some of the confusion that exists as to the relationships of some of the Pliocene porpoises is caused by resemblances due to this common origin. In any event, an extinct killer whale *Orcinus citoniensis* (Capellini, 1883) occurs in the Middle Pliocene of Italy. A nearly complete skeleton, skull, and mandibles of this porpoise was found at Cetona in Tuscany. It has 14 teeth in each jaw, while the living killer whale has from 10 to 14.

In a similar manner, we may trace back the ancestry of the living porpoise *Steno* with a moderately long rostrum to the Middle Pliocene *Steno bellardii* (Portis, 1885) found near Asti, Italy, and the Lower Pliocene *Steno gastaldii* (Brandt, 1874) from the Piemonte district of Italy.

Slender-snouted porpoises belonging to the subfamily Stenodelphininae differ from those referred to the Delphininae by having pterygoids with large reduplications, which overspread the corresponding alisphenoid, and separate cervical vertebrae. The telescoping of the skull has proceeded along the same lines as in the Delphininae. It is fairly certain that their geological history dates back into the Miocene, and that they represent a line of descent that has paralleled the long-snouted porpoises of the Miocene. Their remains have not been recognized as yet in the Miocene formations, and it is not until the Lower Pliocene that we are aware of their presence in former pelagic faunas.

Pontistes rectifrons (Burmeister, 1885) is represented solely by a cranium, lacking the distal portion of the rostrum and the teeth, but otherwise quite complete, found in the Lower Pliocene marine deposits on the bank of the Parana River near the town of Parana, Argentine Republic. The skull shows a striking resemblance to the living *Stenodelphis*, but is twice as large in all its dimensions. It agrees with *Stenodelphis* in the squared occipital region, elevation of the premaxillaries in front of the narial passages, rather slender and somewhat pointed zygomatic processes placed far forward, and slender rostrum. The main differences as far as regards the superior aspect of the skull are that in *Stenodelphis* there is a more obvious side to side constriction of the interorbital region and the lateral margins of the maxillaries are turned upward above the orbits. Furthermore the teeth are about one-third as large and are more closely approximated. A small fragment of the rostrum of a Pleistocene porpoise recently found at San Diego, California, shows so close a resemblance to *Stenodelphis* that it tends to confirm the former existence on the Pacific Coast of a member of the subfamily Stenodelphininae. The teeth of *Stenodelphis sternbergi* (Gregory and Kellogg, 1927) have the same peculiar shape as those of *Stenodelphis*, having an axe-like root and a slender crown, but are less closely spaced. The living member of this subfamily, *Stenodelphis blainvillei*, survives in some of the fresh water streams of Argentina, Uruguay, and Brazil.

(To be concluded)

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RECENT DEVELOPMENTS IN THE PHILOSOPHY OF BIOLOGY

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INTRODUCTION

The immutability of philosophical thought meets the changefulness of the science of biology in that difficult region, which is yet so attractive, the abstract aspects of the study of living things. The philosophy of biology, as it is usually called, is a most unsatisfactory name, for it implies that the philosopher may be defined as the reverse of the specialist who knows continually more and more about less and less. But philosophy is to be understood here in a much wider sense than metaphysics, and must be thought of as part of the theory of scientific investigation as a whole, the self-criticism of the scientific method, and the fascinating attempt to prophesy before the event whether indeed all the realm of living phenomena will follow the inorganic world into the obedience of mathematics. Nobody doubts that Laplace's calculator could have known all about the geology of our era, but whether he could have predicted the constitution and behavior of our standard white rats, and what they think of our feeding experiments, is another matter, and a point of faith on which many a biologist would prefer to be silent.

Reassessments in philosophy are only needed once or twice in a century, though in biology special journals called Reviews have to be provided entirely for them. Progress in the theory of biology stands midway between these extremes. Unlike philosophy proper, the theory of biology is by no means independent of experimental results, although it is true that it needs a very well-aimed stone to trouble her remoter waters. But as will be seen in the reassessment that I propose to make in this paper, now and then experimental results do appear that exercise a very definite influence on the development of the philosophy of biology. Indeed, in the last resort, since we deal here with matters that are more scientific than metaphysical, the final appeal will be to the facts and not to reason, for the biologist like any other scientific worker must be an empiricist to the end.

THE CONCEPT OF THE ORGANISM

The theoretical standpoint that can best be called "Organicism" is probably the most important factor in these considerations at the present time. The word was originally coined by Delage (11) for his great work on biological theory and was used by him in connection with the ideas of Bichat, von Baer and Roux. It was, however, given an entirely new lease of life in 1917 by J. S. Haldane (19), who then used it to describe his own views. These are so familiar to biologists that there cannot be any necessity to repeat them here; it will suffice to say that for him the

living organism as a whole with all its complicated phenomena of regulation presented features that it was impossible to imagine in any constellation of purely physico-chemical processes. The tendency of the organism to maintain its external and internal environments absolutely constant at its own optimum, the *vis medicatrix naturae*, and the preservation of individuality in living organisms, all were adduced by him as examples of phenomena so different from those of the inanimate world that conceptions quite foreign to physics and chemistry would be necessary to account for them in a reasonable manner. Moreover, he felt strongly that these conceptions were in a sense more profound than those of mechanics, and in 1919 he thought it right to maintain that far from physiology being reducible to physics and chemistry, the latter might be reducible to the former. "That a meeting-place," he said (20) "between biology and physical science may at some time be found, there is no reason for doubting. But we may confidently predict that if this meeting place be found, and one of the two sciences is swallowed up, it will not be biology."

This theme, like so many others in these regions was not quite new and had had some interesting historical relationships. Cagniard de Latour and others, for instance, had difficulty in persuading biochemists of the necessity of the yeast-cell in fermentation, owing to their distaste for attributing chemical processes to "vital activity." As a prophecy it has borne fruit very much more rapidly than that famous one of Kant's about the blade of grass, though as in that case we still cannot be sure whether the true messiah has arrived or no. Fulfilment of Haldane's prophecy may perhaps be seen in the fundamental work of A. N. Whitehead, who in his book *Science and the Modern World* (56), sets out an organic theory of nature. Still more recently a most lucid commentary and amplification of his suggestions has been given by C. Lloyd Morgan (39). The concept of the organism is now carried over into the inorganic world, and the whole universe is regarded as being made up of organisms, some of greater complexity than others but all possessing the properties of organisms. The distinguishing feature of an organism is that its parts are not entities having a full existence by themselves, but rather owe their being to the whole of which they form parts—so that if the whole is taken to pieces, the parts entirely cease to be what they were. Each part is what it is not in its own peculiar right, but by virtue of its relatedness to all the other parts in the whole. Already in *Life, Mind, and Spirit* (38), Lloyd Morgan had maintained that this kind of relatedness of parts within wholes was not a criterion of living things sufficient to distinguish them from non-living things, and A. N. Whitehead has worked out in great detail the concept of the organism in the physico-chemical world. To say that there is the same kind of internal inter-relatedness about physico-chemical organisms as about living organisms or social organisms is not to assert that there is no difference between these sorts of organism. The most extreme of the old-fashioned biological materialists never denied that there were differences between living animals and inorganic systems, for that would have been too obviously contrary to common sense; he simply said that the differences were of degree and not of kind, that the former, in a word, were only complicated special cases of the latter, whereas his opponents definitely brought in something new.

It is this in the modern extension of the concept of the organism that is so impor-

tant for the theory of biology. It means—if recent "organicism" is justified and maintains the positions it has gained—that another middle line of partition between living matter and dead matter is to be abandoned. There have been many of them, but none have withstood the advance of exact biology. If this process is followed historically it can be seen how the two most obstinate and irreducible characteristics of life were its finalistic or teleological aspects and its special arrangement in organisms, entities with a high degree of internal relatedness and dependence. The former of these has vanished with the realization of the teleology of the inorganic world, an event that will always be associated with the name of Lawrence Henderson, and now the latter would appear also to be universally present throughout nature. "Some biologists" says Lloyd Morgan (39) "interpret all organic action in the modal terms appropriate to physics and chemistry, others there are whose interpretation is couched in the modal terms appropriate to psychology. It is difficult to see on what logical grounds biologists of the first school—the so-called mechanists—can resent the downward extension of the connotation of the word 'organism' to natural entities which as they claim differ only in their lack of superadded complexity and no wise essentially in type of action or behavior. It is, however, easy to see on what logical grounds biologists of the other school—the so-called vitalists—can resent, and will no doubt reject, a concept of the organism which implies that it can adequately be discussed in terms of an organic theory of nature without introducing any further concept such as entelechy or élan." I suggest that the discovery of the value of the concept of the organism in the philosophical aspection of physico-chemical phenomena, is of great importance for the theory of biology. Workers in exact biology would in any case have had to go on using mechanism as a working principle in research, because as is well known it is the only one that will work; but it will relieve them to learn that the concept of the organism is no longer purely biological. The field of physics and chemistry, which was formerly covered by the mechanistic schema, continues to be so covered, only now the concept of the organism covers it also. Whereas until recent times, mechanism was held to be the only way of interpreting physico-chemical phenomena, while there was great doubt as to whether mechanism or organicism was the only way of interpreting life phenomena, now both mechanism and organicism come into force over both domains of experience. In other words we have to deal not with two opposing and incompatible modes of explanation struggling between themselves for fragments of our experience, but rather with two complementary and different modes of explanation covering the entire expanse of living and nonliving things. If we reserve the name of science for the mechanistic mode of interpretation we shall only be obeying a necessary outcome of the quantitative and metrical character of the scientific method, and organicism, covering both realms as it now claims to do, we shall term a philosophical theory. Thus to the scientific mind the living and the nonliving form one continuous series of systems of differing degrees of complexity, all of which consist of parts that can be understood as parts when separated from their wholes and are therefore interpretable in terms of "metrical macroscopic mechanism;" while to the philosophic mind the whole universe, itself perhaps an organism, is composed of a vast number

of interlacing organisms of all sizes. Organisms explode into nothing when taken to pieces, systems remain in the form of parts the relations of which can be understood. In this way the incurably analytic character of science contributes its force to the conclusion that anything may be subjected to scientific study but nothing sucked entirely dry of significance by so doing.

Thus if J. S. Haldane's prophecy has been fulfilled, it is not without a certain irony. Physics has not swallowed up physiology nor on the other hand has physiology swallowed up physics; they have devoured each other and of the old antithesis nothing is left.

To what extent the relegation of the concept of the organism to philosophy is absolute must still, however, be considered a little uncertain. In spite of its history as measured in years, the concept is still so young that we are not yet sure whether there is a sense in which the term would be applicable to a scientific hypothesis pure and simple. It is just conceivable that organicism might stand in the peculiar position of being a scientific hypothesis as well as a philosophical theory. The most important factor in this situation is the work of C. D. Murray (40, 41). In several recent papers this physiologist has applied the principle of minimum work to physiological organisms, and his success has already been very considerable. In Murray's view, the concept of organization is definitely not an "affair of the reflective judgment" but a very legitimate field for scientific experiment and calculation. Murray considers that at least two statistical laws may be obtained from the study of living organisms, both of which afford a quantitative expression of the complex systems in question. The first of these he terms the "principle of maintenance of steady states"—this would correspond to the maintenance of constancy of external and internal environment—and the second, the "principle of minimum work." This second principle states that the cost of operation of physiological systems tends always to be a minimum, and thus is an extension of the well-known principle of Lagrange. Murray works out this conception in its relations to the physiology of the circulation and gives a preliminary answer, at any rate, to the question, "In any extra effort by the organism as a whole, how is the tax or effort distributed among the various organs of the body (the parts of the whole) and what does each contribute to the extra effort of the whole?" This is certainly a most important section of the problem of organization. The principle of minimum work has the great value of defining mathematically the distribution of function among the parts of the organism. But the undecided question is, whether the word organism means here the same thing as it does in Whitehead and Lloyd Morgan. It is very doubtful whether it does, for an organism in their language means a whole that does not exist dismembered in the constituent parts, and can only be understood as a whole. There would appear to be three ways at least of thinking about a bicycle, (a) to regard it as an object capable of movement and only truly seen in its wholeness (Whitehead and Lloyd Morgan), (b) to analyze it in the confidence that the relation between the parts can be understood in isolation and systematically 1. without actually taking it to pieces (Murray) and 2. with actual analysis (the majority of biophysicists and biochemists). In any case, the slight residuum of organicism left behind in science by the transplantation of the concept of the organism into a general philosophical theory of nature will no doubt be readily

dealt with by the scientific method. Summed up as it is in Wordsworth's "We murder to dissect" organicism is certainly far from characteristic of the scientific mind.

LIVING MATTER AND THERMODYNAMICS

The relations of living systems to the law of entropy have been considered again and again during the last fifty years, and now very recently the question has been reopened by F. G. Donnan. That living things should be in some way exempt from the otherwise universal law that free energy tends always to decrease in amount in the known universe and entropy to increase, has many times been asserted, though without any evidence. The earliest hint of this is found in the writings of Lord Kelvin, then Sir. W. Thomson, who said as long ago as 1852 "It is impossible by means of *inanimate* material agency to derive mechanical effect from any portion of matter by cooling it below the temperature of the coldest of surrounding objects" (52). Thus, as Guye says, Thomson was already making reservations on the applicability of Carnot's principle to the mechanism of living systems. Then in 1882 H. von Helmholtz (24) definitely suggested that living cells might have some way of eluding Carnot's principle. In a paper read before the Berlin Academy of Sciences on February 2 of that year he said in a footnote, referring to the impossibility of any increase of free energy: "Whether such a change would also be impossible in the fine structure of living organized tissue appears to me still to be an open question, the importance of which in the economy of nature is very obvious."

Here there was already the hint of the mechanism by means of which this might be done. The appreciation of the statistical nature of the second law, gave it, however, much greater precision. James Johnstone (29) and G. N. Lewis (31) more recently both decided that living things and living things alone can retard the accumulation of entropy. Now obviously the most astonishing things may be hidden by statistical treatment. Somewhere in the universe water may run uphill, though as a whole, and in general, it does not do so. The treatment of men on a statistical basis furnishes results of great value, but there we know directly and by observation how individual the individual is. This may be also the case with molecules, and it is a commonplace that to an intelligence such as a Clerk-Maxwell demon they may have very pronounced individuality. As G. N. Lewis says, there is certain astronomical evidence that indicates the existence of disentropic phases in the universe, phases in which the amount of bound energy is diminishing instead of increasing; it is, therefore, equally possible that in the living body there are also phases where the statistical second law does not truly apply. That living plants retard the accumulation of entropy by storing free energy is undeniable, but that any living system ever reverses this process is another matter. Nevertheless both Johnstone and Lewis regard it as the main characteristic of life, as does Driesch (13), who says "Es gibt seine Dämonen. Wir selbst sind sie!"

In 1919 Guye (17) devoted some space to the examination of this question. He showed clearly that the high efficiency of physiological systems in no way proved that they functioned contrary to Carnot's principle, but rather that they were not true heat engines, a fact quite well appreciated by physiologists. He also demonstrated that the retardation of entropy-increase by the green plant was a process that could be paralleled in several non-living systems, for instance, the evaporation of the oceans.

But the realization of the statistical nature of the Carnot principle had certain implications for biological theory. If the law of entropy may justly be compared to the law that a large and equal number of black and white grains shaken up will produce a grey powder, then two considerations emerge. Firstly, the sorting out of the grains could be accomplished by a Maxwell demon—in Lewis' terminology, a cheat—acting in the system, and secondly, by prolonging the agitation till a fluctuation of a very rare type led back to the original condition, on the basis of Heraclitus' remark—"If one is sufficiently lavish with time, everything possible happens"—surely not due to Herodotus as Guye would attribute it. This reminds one of F. R. Japp's refusal (27) to believe that if a font of type was shaken up in a bag, the text of Hamlet could possibly result, however long this was continued, and of P. F. Frankland's reply (14) that if the time allowed was infinite, Hamlet must result. What is sure, at any rate, is that the statistical nature of Carnot's principle does not preclude such a rare fluctuation, nor less rare minor ones tending in the same direction. As Johnstone said, a philosophical consideration of this subject must take into account chances which even an insurance company would at once set aside as of no matter. Now "The fluctuations," says Guye (18), "which can occur in a given element of volume are in general the more important the smaller the number of molecules contained in the homogeneous element of volume considered. The reply to the foregoing question will depend therefore, on the degree of tenuity which is attributed to the structure of the tissues and of the living matter."

This is, indeed the aspect of the question that has recently been engaging attention. A. V. Hill (25) came to the conclusion recently that "It is conceivable that the ultimate minute mechanism especially of the smallest living cells, may somehow be able to evade the statistical rules which govern larger systems; it may for example like Maxwell's demon be able to sort molecules, to use the energy of the more rapidly-moving, to employ a unidirectional permeability, and so to avoid the general increase of entropy which appears to be the governing factor in all other material change. Such an evasion, if established, would be of ultimate philosophical, biological, and practical importance; there is no evidence, however, of any value, that it really occurs." F. G. Donnan (12), on the other hand, has recently made some calculations which if they do no more, at least keep open the possibility; he has attempted to estimate the size of the element of volume within which an evasion of the second law would be likely to take place. He shows how for all ordinary cases the probable fluctuations from the equilibrium state would be quite imperceptible, in other words, the chances would be immeasurably against any deviation from Carnot's principle. But for a small cubical particle of side 0.1μ consisting wholly of molecules of molecular weight 10,000 the relative thermodynamic probability of an easily detectable fluctuation from the chemical equilibrium state is distinctly high. As Donnan points out, although it is true that most living cells are larger than the imaginary particle in question, some are not, and probably it does not materially differ in size from phases and parts of cells having separate existence as systems to say nothing of the bacteriophage and ultrafiltrable viruses. "It seems, therefore," he says "very probable that there exist biological systems of such minute dimensions that the laws of classical

thermodynamics are no longer applicable to them. Such laws must be replaced by the statistical theory of molecular fluctuation and in the last resort by the theory of individual action."

It must be noted that to admit this is not to go so far as Johnstone and Lewis, who assert the existence of disentropic phases within the living cell. The question may, moreover, be approached in another way. If a machine, living or otherwise, is perfect it should yield up the same amount of work as is put into it, in other words it should waste nothing of the driving force supplied to it. The ratio between the energy put in and the energy got out may be called the "free energy efficiency" of the process, and obviously for a perfect machine this should be unity or 100 per cent. For a system containing an imaginary being such as Maxwell's demon, capable of defeating the second law of thermodynamics by causing a decrease in entropy the efficiency would be greater than 100 per cent. For all known machines it is less than 100 per cent. The parallel between the numerical figure for the efficiency of living and non-living machines is often very close. To compare the animal to a heat-engine, is, as Guye points out, misleading, for the energy of the steam engine is changed in form as it passes through it, but the comparison between the growing animal and a boiler or an electric battery is much closer. The "apparent energetic efficiency" of the developing embryos of the chick, the silkworm, the minnow, and the frog has recently been calculated (Needham (42)) and works out on the average to 77 per cent. This means that out of 100 gram calories presented to the organism in the form of yolk and white 23 have to be wasted and 77 can be stored. Similarly, the business of the electric accumulator is to store energy and this cannot be done with an efficiency greater than 75 per cent (Davidge and Hutchinson (10)). The boiler, again, is designed to transfer as much heat as possible from coal to steam, but this can never be done with an efficiency greater than 77 per cent (Brownlie (4)). It is doubtful, however, how much stress can be laid on any numerical correspondence between the efficiency of the growing embryo and such non-living machines.

What of course would show up the presence of the Maxwell demon in living matter would be an efficiency greater than 100 per cent. Such an efficiency has never been reported for any of the higher animals under any conditions, but it might be thought that the place to look for it would be the iron and sulphur bacteria, maintaining as they do a precarious existence on the most unpromising foodstuffs. This problem has recently been considered by Baas-Becking and Parks (1). They have calculated the free energy efficiencies of many forms of autotrophic bacteria, and though here, if anywhere, living matter might be expected to need demonic assistance, the efficiencies were always very low. The hydrogen bacteria operated at an efficiency of 26 per cent, the methane bacteria at 30 per cent, the nitrite-forming bacteria at 6 per cent. As for the sulphur bacteria the figure obtained was 8 per cent, and for the iron bacteria (supposing that such organisms really exist) it would also be very low. These observations certainly seem to be in favor of the views of Hill and against the possibility indicated by Donnan and assumed to hold in practice by Johnstone, Lewis, and Driesch. But it must be remembered that an appeal to colonies of bacteria gives no less a statistical result than the appeal to Atwaters' calorimeter. Reference must here be made to a very important recent paper of R. S. Lillie's (34). Lillie

suggests that the existence of rare disentropic phases in living matter, where infractions of the second law can go on might account for the subjective persuasion of freedom which all men have and so introduce a kind of free-will into the structure of science itself. He points out that if such intracellular phases may once with reason be postulated, there is no difficulty in imagining their effect on the body as a whole, in view of the extraordinary capacity which the body has of transmitting changes of state from one point in space to another. In this way a voluntary action would arise from an individual escape from the second law in one of the ultramicroscopic intracellular phases in the living being. But is infraction of the second law the same thing as a breakdown of scientific determinism? Lillie passes by an insensible transition from the latter to the former, but perhaps this is not justified. Does scientific determinism—in so far as it is not confused with scientific naturalism—make any claim to be more than statistical? If in the scientific formulation of things, the individual always escapes, then anything that individual atoms may do in the ultimate recesses of the animal body is metaphysical in the truest and most literal sense of the word.

Lillie himself refers to the expression "physical indeterminism" as a misnomer, and admits that though the laws of the microscopic may not be the same as the laws of the macroscopic, there must be laws of some sort there. And if that is the case, it is difficult to see how on a scientific basis *alone* there can be any spontaneity or freedom. Thus if we suppose that escape from the second law regularly takes place in the intimate structure of living organisms, it will surely not be escape into freedom but into the arms of some wider statistical law inevitably brought into existence by the operation of the scientific way of thought. Or, in other words, the inductive method will again assert its supremacy and nothing will escape from all this save what always did escape, namely, individuality. The unique is the only nut that science cannot crack, and freedom implies uniqueness.

Lillie's paper may be said, then, to push back individuality into the disentropic phase, and not, as its title would imply, to reconcile indeterminism with science. But an altogether fresh wind blows through his memoir in question, and it is significant that he draws attention to the importance of the quantum theory for the philosophy of biology.

Thermodynamical considerations have recently led to the partial solution of one problem which was brought greatly into prominence in neo-vitalistic discussions. The extraordinary fact that the swim-bladder of fishes living at great depths contains nearly pure oxygen was first discovered by Biot (3), who analysed the gas during a scientific expedition and had his eudiometer broken by the explosion. "As nearly pure oxygen" said Haldane (20) "has been obtained from the swim-bladders of fishes living at a depth of 750 fathoms (4500 feet), it follows that oxygen may be secreted into the swim-bladder and retained in it in the gaseous form at a pressure of over 120 atmospheres, whereas the partial pressure of oxygen in the surrounding sea-water is only about one-fifth of an atmosphere. It seems perfectly clear, therefore, that the liberation of oxygen and its retention by the semi-liquid wall of the swim-bladder is the result of an active physiological process in the living cells lining its walls, and cannot be explained mechanically." F. J. W. Roughton (47) has recently suggested that on the contrary

no necessity need be felt for a complete abandonment of mechanical explanation in this case. If the specific heat of the reactants and resultants of a chemical reaction is known, the equilibrium constant can be calculated by the use of Nernst's equation. Now if the equilibrium constant of the reaction $H_2O_2 = H_2O + O$ catalysed by the enzyme catalase be calculated it works out at $10^{18.4}$ from which it may be concluded that not 120 atmospheres but billions of atmospheres would be required to suppress the production of oxygen from hydrogen peroxide by the enzyme catalase. With this most interesting demonstration there collapses one of the most formidable of the objections on which the neo-vitalists have been accustomed to rely. Haldane (21) has recently given a historical review of the famous controversy about secretion and filtration of oxygen in the human lung, and concludes still, as against Barcroft, that only the secretion-theory can explain the facts of acclimatization to life at high altitudes. These questions give additional significance to Roughton's calculation.

REGULATION IN LIVING MATTER

The finalism associated with living beings is nowhere more insistently evident than in their unswerving maintenance of steady states. The living organism has as it were a certain niche in its physico-chemical surroundings, and to that it will always return provided that the disturbing influence has not been so great as to throw it out of gear altogether. Its normal hydrogen ion concentration, its normal osmotic pressure, its normal concentration of glucose or salts, its normal physiological constants, these it will always tend to preserve unchanged. The purposiveness with which it clings to this equilibrium has to be disregarded altogether as such in the application of the scientific method to life phenomena, for teleology is not a concept in any way congruent with measurement. An interesting attempt has indeed been made by Lillie (32) to give biological purposiveness a quantitative expression by regarding it as a special case of equilibrium, namely between organism and environment, and so applying to it an extended form of the principle of LeChatelier. In spite of Lillie's excellent discussion, however, in which the balance between the constructive and constitutive on the one hand and the destructive and dissipative tendencies in living things on the other are so well set forth, it is still extremely uncertain whether the concept of teleology can be translated into mechanical terms. It is more likely that these principles are inherently antipathetic. Probably they cannot with advantage be mixed.

But the phenomena of regulation of steady states in living things may be approached from a purely scientific angle. The importance of buffer action was amply appreciated by Lawrence Henderson, and it will be remembered that in the preface to his book *The Fitness of the Environment* he says that he was led to those considerations by researches on the special properties of solutions of phosphates and borates. Buffer action, indeed, must be regarded as a most important factor in organic regulation. The phenomena of oxidation-reduction potential have been also much studied of recent times, and here again systems have been discovered in which an addition of one of the reactants produces a minimum change in the state of the system as a whole. Such conditions are discussed in the papers of Mansfield Clark and his colleagues (6), and to the phenomenon Clark has given the name "poising action" to indicate its similarity to buffer action in the case of hydrogen ion concentration.

The importance of these advances for the general theory of biology does not seem to have been sufficiently considered. Driesch's expression "a harmonious equipotential system" undoubtedly seemed impossible to imagine on a mechanical basis at the time when he introduced the term, but there is now not the same justification for pessimism. It is becoming clearer and clearer that the living cell exists in an extremely balanced condition, well buffered, heavily poised, apt in every way to resist influences tending to move it out of its equilibrium position. Unsuccessful attempts were made some years ago by L. T. Troland (54) to relate the phenomena of regulation in living cells to the properties of enzymes, but though these failed in detail he was nevertheless on the right track. We may conclude that it is possible, already and in spite of the great incompleteness of our knowledge of biophysics and biochemistry, to point to purely physico-chemical systems that would be bound to exhibit, when working in intimate association, simple forms of that tendency to constancy of internal and external environment which the neo-vitalists regarded as preeminently the god in the machine.

It is worth while also to study in this connection the exact limits of regulation power, for Lillie's question—"Why can the salamander-entelechy regenerate a leg but not the cat-entelechy?" has lost none of its force. In embryology the researches of Spemann and his school, reviewed recently by Huxley (26) and de Beer (2), have done much to clear the air. The totipotence of the early embryo, or rather, the approximation towards the state of totipotence, which is then observed, falls off rapidly as development proceeds, and by the time of gastrulation the process of chemo-differentiation sets in. After this, all development is irrevocably determined, ectoderm cells will make ectoderm and nothing else, until finally in the very late stages regulation of form again becomes possible, owing to the assumption of function; this is the stage of Roux's "struggle of the parts." "The inability of organisms to regulate during the period of self-differentiation of different organs can be illustrated by the analogy of an army," says de Beer, "whose staff at the outset of the campaign has determined and assigned the duties of the various corps. It loses control of these while they are independently performing their allotted tasks, and regains it again later when inter-communication is reestablished. The amazing results of regulation in Clavellina, sea-urchin blastomeres, etc. have led to the forms of vitalism which have been developed by Driesch and others. It is therefore interesting to find that organisms do not always regulate."

MINOR CONSIDERATIONS

An interesting suggestion as to the nature of tonus and trophic action in living organisms has recently been made by Sir W. B. Hardy (22). The manner in which nerve fibres control tonus and heat-production in muscle, for instance, has always been exceedingly obscure and has furnished a theme for several neo-vitalist physiologists. It is indeed true that while we have considerable information about the waves of nervous excitation which produce muscular movement, we know nothing at all about the nature of trophic action and the control of tonus in muscle. Hardy suggests that the explanation may probably be found in the orientation of molecules, a process which can certainly happen in masses of matter though it has been mostly studied in surface films. Experiments with lubricants demonstrate that layers of ori-

ented molecules may be several thousands thick, and though this is, as Hardy says, an insignificant example beside the colossal ones furnished by the living organism, yet it is the first likely explanation of trophic action that has been advanced and thus removes from physiology the stigma of having absolutely no explanation at all for such phenomena.

Reference may also be made to the monograph of Hedges and Myers (23), who have collected together a great deal of information about periodical reactions in pure chemistry; reactions which exhibit rhythmic pulsation or intermittency. The most famous example of such a reaction is probably the formation of the Liesegang rings. This book forms the most considerable addition of recent times to the literature concerning "simulacra vitae," already very considerable in extent. Although it is true that from a philosophical point of view the significance of these imitations of living processes can easily be overestimated, yet they have a certain value, and the more they accumulate, and the more complicated they become, the more difficult it is to hold the views of Haldane, Driesch, or Rignano. It is much to be wished that some historian would collect the many data in existence about "simulacra vitae" beginning with Roger Bacon's speaking head and passing through the automaton chess-players of the time of de la Mettrie to the selenium dog and Lotka's mechanical beetle.

Finally, a word might be said with advantage about the supposition that the biologist is always, if the truth were told, a thanatologist and that biophysics and biochemistry are simply the study of dead matter which had once been alive. This belief is common; for example, Johnstone (29) says "Remember the (easily ignored) fact that of living substance we literally know nothing. We study the behavior only of the living organism. Whenever we study organic substance, it is necessarily dead inert material that we investigate." Such inaccurate statements may surely cause great misapprehension in the minds of laymen. Physiology and biochemistry have never been restricted to examining dead animals, and as technique develops they do so less and less. As instances the work of Chambers (5) and others (45) might be given, in which indicators are injected into living cells, or Gelfan's (15) micro-electrodes used in a similar manner, or again, Seifriz's (48) determination of protoplasmic viscosity by means of an exceedingly minute metal ball introduced into a single cell and then caused to move towards an electro-magnet. Vlès (55), moreover, has determined the intracellular pH by spectroscopic and spectrophotometric methods involving no interference with the living cell at all. The constitution of plant tissue has been examined with x-ray analysis by Sponsler (50), and Crozier (8) has shown what far-reaching conclusions about the metabolism of living animals can be drawn from a study of the effects of temperature upon them, as may also be seen from the beautiful work of O. Glaser (16), which caused no greater inconvenience to his paramoecia than getting them to swim through a glass tube at different temperatures. There can be no doubt that as biological methods become more refined, the injury caused to the experimental material will become ever slighter.

CONCLUSION

It will not be very difficult to outline shortly the direction which the trend of thought in the philosophy of biology is at present taking. The neo-vitalist school, which some years ago seemed to

have the future in its own hands, has not been able to live up to its promises. The more its special entities immanent in living beings have been considered, the less necessary they have seemed to be in relation to the facts and the less valuable they have been found as inspirations to research. The finalist school with its insistence on teleology as the special sign-manual of life has been unable to deny the teleology of the inorganic world, so that the Aristotelian conception modified by Kant of the efficient cause and the final cause as two complementary explanations of all natural phenomena remains unsuperseded. The older organicism, which saw in living organisms an interrelatedness of parts present nowhere else in the universe, has been swallowed up in an organic theory of nature which regards all things, and even all events, as themselves organisms. The classical biological mechanisticism with its roots invisibly but surely embedded in the naturalistic view of the world has withered away altogether since the general abandonment of the notion that the application of the scientific method exhausted the content of things. And lastly, the psychobiologists, who asserted that biology could only be made intelligible by employing psychological concepts at all points, have failed to commend their views by producing a serious body of experimental work.

Out of the decay of these theories—valuable as they certainly were in their day—have arisen various standpoints one of which has come to be called "Neo-mechanism" (43). It is represented by a variety of biologists and others (53, 37, 9, 28, 33, 36, 35, 46, 49, and 51) who all agree in regarding the scientific method as essentially mathematical, mechanical, deterministic, quantitative, abstract, and by consequence inapt to include the entelechy or any similar conception; and with all this, at the same time a partial, distorted, and as it were twisted approximation to truth. The neo-mechanistic position, therefore, at one and the same time asserting the universal dominion of the mechanical sort of explanation over all nature, living and non-living, and admitting the inadequate nature of this sort of explanation as a full account of the world, resembles the old mechanisticism in maintaining the heuristic need for the machine, and differs from it in seeing nothing solely ultimate about the machine. It thus recognizes itself to be the way the scientific mind goes to work, and not the manner of thinking in philosophy, theology, or art. It differs of course completely from neo-vitalism in denying the bare value of any entelechy or archaeus in living things; it can have nothing to do with any elasticity in its laws, and deprecates that παρέγκλισις which Lucretius was weak enough to introduce into his world.

> " . . . . incerto tempore ferme incertisque locis spatio depellere paulum, tantum quod nomen mutatum dicere possis."

It also differs from biological finalism, for it knows teleology to be an unquantitative category, and banishes it from the laboratory to the domain of the philosophers, who are quite capable of dealing with it. It welcomes the organic theory of nature, for to the exact biologist, nothing is an organism any more than anything else; to the philosopher, all things are organisms, and just as the scientific mind sees different degrees of complexity in its systems, so the philosopher sees emergent degrees of complexity in his organisms, up to the world-soul itself. The neo-mechanistic position stands in close relationship with the views put forward by R. G. Collingwood in his recent book

Speculum Mentis (7), and for a statement of the theory of science here adopted, the chapters on science in his work are much more than adequate. It is easy to see how the experimental advances which have been collected together in this paper fit in with the neo-mechanistic attitude. The organic theory of nature, which seems to have so great a future before it, is the natural counterpart in philosophy of neo-mechanism in biology and what we know of the thermodynamic aspects of living things gives us little reason for supposing that the laws we have now are likely to break down in biology in the future. Neo-mechanism gives biological science all it wants and at the same time is not easy to attack from a philosophical angle, for the simple reason that it makes no philosophical claims.

It may be noted that such a standpoint will not necessarily object to special "biological" laws or explanations, provided that these are clearly understood to possess an "interim" character and to be only awaiting expression in physico-chemical terms. There is no harm in classing the poppy with other therapeutic plants as having the "virtus dormitiva" of Galen and of Molière, provided Overton's theory and all its more accurate successors follow close behind. To say that opium possesses a "dormitive faculty" is a mere restatement of the facts but to say that it does so because morphine is fat-soluble is at least intelligible even though it may not be true. It promises truth to come. But this is not to admit the value of "special biological laws" conceived in terms of "activity, purpose, values" etc. and never intended to be reduced to physico-chemical intelligibility. Such generalizations as these still find defenders, e.g. J. H. Woodger (57). "Because mechanics," he says, "quite rightly banishes 'force' and 'activity' from its conceptual equipment as mere anthropomorphism, is it correct to turn this deanthropomorphizing process on ἄνθρωπος himself?" The answer is yes, if ἄνθρωπος is to be an object of scientific study, for a strenuous tendency against projections of ourselves into the external world is one of the principal characteristics of the scientific method. There exists here a confusion of philosophy and perhaps theology also with science which has caused much trouble in the past and will cause more. Ἄνθρωπος not deanthropomorphized is a mixture of all kinds of experience, exact biology, philosophic speculation and argument, religious and artistic appreciation, historical understanding. In so far as he is the object of scientific thought, he must be deanthropomorphized: and the legitimate aversion to paradoxes which we all feel kept within bounds.

If, then, for the biologist neo-mechanism seems to fit in best with recent tendencies in the theory of the study of living things, the future becomes clearer than before. There is nothing save the inherent difficulties of research to hinder the advance of exact physico-chemical methods in biology, and these obstacles have never yet daunted the enthusiasm of investigators. It was the paper lions of vitalism in their path that made them hesitate; the fruit of minds overprone to regard as inexplicable that which has not been explained. At the same time, the frank rejection of that philosophy which regarded the scientific method as the only one capable of revealing truth establishes the claim of modern biology to metaphysical respectability. Biology can claim to be well aware of the limitations inherent in the method of science, and of the illimitability of the subject-matter to which it can be applied.

James Johnstone, in a recent paper

(30), has adopted the neo-mechanistic position, which is all the more surprising in that his former works could accurately be described as a "skilful blend of Driesch and Bergson." But now he says "It is a plain and very obvious fact that we have built up our societies and social relationships on the basis of quite irrational recognitions of life in other things than ourselves, and it is very curious that we should refuse to consider this experience as part of that which can be explained in physical terms. Yet it is quite certain that biology will never abandon its mechanistic attitude. The latter is something more than merely an hypothesis, it is a demand or an ideal of explanation which we insist upon in our investigation of life activity." It is, in a word, one of the fundamental ways in which we think, and its apriority is something which we cannot possibly get behind. "Mathematics, mechanics, and materialism," as R. G. Collingwood puts it, "are the three marks of all science, a triad of which none can be separated from the others, since in fact they all follow from the original act by which the scientific consciousness comes into being, namely, the assertion of the abstract concept." But science is not the only activity of the human spirit.

There is indeed all the difference in the world between pushing mechanistic explanation as far as it will go with the realization that it will go all the way but will not entirely satisfy you when you have got there, and diluting it with other (qualitative) sorts of explanation, in the hope that the mixture will afford you full satisfaction. It is this latter process that is being given up in biology. Scientific explanation and philosophical explanation are two distinct foods of the soul, and they are confused only at great peril. Or, in the words of an immortal limerick due to Charles Inge,

> "There was an old fellow of Crediton,
> Who took paté-de-fois-gras and spread it on
> A chocolate biscuit
> Exclaiming 'I'll risk it!'
> His tomb gives the date that he said it on."

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CEPHALOPOD ADAPTATIONS—THE RECORD AND ITS INTERPRETATION

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IT SHOULD be recognized at the outset that the present paper is highly speculative in character. Not that the author has much faith in such a method of attacking a problem, but, as will appear in the sequel, because this is the only method of approach in any consideration of the probable structure of the soft parts or habits of life of the extinct representatives of this very important class of the Mollusca.

The abundance of fossils of this class in the English midlands, where William Smith first developed the idea of stratigraphic succession, their similar abundance in the historic eastern Alps and elsewhere in Europe near centers of scientific population, early stimulated speculation regarding the characters of the inhabitants of these fossil shells, and so much has been written upon this subject that it is doubtful whether any of the ideas advanced here have not already been proposed in one form or another. I have tried to acquaint myself with the literature, but will not attempt citation in most cases, contenting myself with the foregoing disclaimer of originality.

The Cephalopoda, whose ancient line extends over at least a hundred million years from the oldest known forms of the Cambrian period to the present, and which easily comprises upward of 10,000 known extinct species of great variety of form and presumably of habits, is represented in existing seas by a single restricted (Willey, 1902, recognizes four species) genus with an external shell—the familiar pearly Nautilus; by the less known monotypic genus *Spirula*, with an internal shell; by the variety of active squids and cuttles, with an internal highly modified vestige of a shell; and by the less active octopus tribe, without any trace of a shell.

Throughout the greater part of the geological record their representation in the rocks will naturally be the shelled forms, which alone furnish the requisite hard parts for normal preservation as fossils. Among these the great group of ammonites, with their highly specialized septa, have been entirely extinct since Cretaceous time. (I do not think that I need waste space in refuting Steinmann's idea that the existing dibranchiates are their direct descendants.) The racial history of the ammonite order extended from the late Silurian to the close of the Upper Cretaceous—an inconceivably long period, during which they developed a multitude of forms, and they were easily the dominant cephalopods throughout much of the Mesozoic era.

Since the existing shell-less forms are geologically modern and show every indication of post-Paleozoic evolution culminating in modern times, they afford but slight basis for comparison with the multitude of shelled forms that go back to the oldest fossiliferous rocks. The

existing Spirula, which is itself related to the ancestral squids, is quite unlike the remote shelled ancient stock; so that the existing Nautilus alone can serve as a point of departure from which to envisage the structure and habits of the majority of fossil forms.

This lack of existing comparable forms has led to serious misinterpretations of extinct forms, stratigraphic and taxonomic paleontologists usually not having seen the forest because of the trees, and has opened the way for a multitude of diverse speculations and generalizations, more often dogmatic than probable. It is proposed in the following pages to pass in review what may be logically inferred regarding the structure and habits of these long vanished races, and it is freely admitted that a single fact of observation may upset a sheaf of deductive philosophy.

CEPHALOPOD CLASSIFICATION

Richard Owen, who gave us an admirable account of the anatomy of the pearly Nautilus in 1832, divided the existing cephalopods into two sub-classes—the two-gilled, shell-less Dibranchiata, and the four-gilled Nautilus or Tetrabranchiata. Paleontologists have rather generally assumed that the extinct nautiloids and ammonoids had four gills as in the single surviving genus *Nautilus*, although the two-gilled forms were obviously derived from the same stock. This assumption is highly illogical and equally improbable. It is not a matter of great moment whether the extinct forms had two, four, or some other number of gills—there is a great amount of diversity in this feature throughout the molluscan phylum; but it is important, it seems to me, not to base their segregation into major groups upon the number of gills when we can never hope to know what the number was in 99 per cent of the cases. The sub-classes of Owen are therefore meaningless throughout all time but the present. The alternative terms Ectocochlia and Endocochlia for the two classic sub-classes are not particularly euphonious, fail to recognize the threefold diversity of the cephalopods, and are most inappropriate, since a considerable number of the Endocochlia lack all traces of a shell, and others—the extinct belemnoids and the existing Spirula—are ectocochlia in their youth and become endocochlia during their ontogeny.

Three subclasses should be recognized, namely: the Nautiloidea, Ammonoidea, and Coleoidea or Dibranchiata—the last largely living, and the fossil forms furnishing enough indications of their soft anatomy in the fine grained muds of the Jurassic to give a fairly clear idea of their structure.

A second rather general misconception of another morphological feature of the extinct animal has been the assumption that since the pearly Nautilus has numerous tentacles, all fossil nautiloids and ammonoids were similarly equipped. We know that in *Spirula*, the existing squids and Octopoda, and the extinct belemnoids, quite a different and more restricted number of more specialized tentacles was universally present, and since these groups were derived from the more primitive shelled stock, the question of whether fossil nautiloids and ammonoids had many tentacles or a few so-called arms is to be determined, if at all, by evidence drawn from the geological record and not from their supposed position in the taxonomic scheme of the systematists.

The keynote of evolution of the hosts of extinct cephalopods, as it appears to me, is adaptation—a thought already ably voiced by Diener. The founders of the more modern study of fossil cephalopods—men like Alpheus Hyatt—were entirely

dominated by a sort of theological philosophy, and particularly by one of the outstanding tenets of the American school of Neo-Lamarckianism, namely: that of racial senescence as expressed in seemingly bizarre appendages or ornamentation, and supposed atavistic simplification of the shell architecture. What could seemingly be more conclusive evidence of senescence than *Baculites*, appearing near the close of the geological record of the ammonites, with its tiny coiled baby shell like that of its ancestors, early forsaking the ancestral plan of rectitude and straightening out into a large orthocone? It would even have an immoral quality in the mind of the late John M. Clarke.

However, since racial senescence, in the sense that the protoplasm, vital force, nucleic control, or whatever you choose to call it, had suffered an old-age devitalization which was responsible for the observed changes in form, is non-existent, some other explanation must be sought, and my answer would be that this was adaptation to new environments or habits. Racial senescence is only permissible as a descriptive phrase for a race, not necessarily old, which is not overly successful in competition with its contemporaries and is therefore dwindling. Such a one, and there are many throughout the history of all fossil groups, is more appropriately compared with a backward human race than with a senile individual. In any case the use of the phrase is not the explanation of the observed changes of form or ornamentation that the fossil record discloses.

THE EVOLUTION OF THE CEPHALOPODS

In the following pages I shall endeavor to give a very much abridged account of the evolution and adaptation of the group, and then discuss a few selected examples in somewhat more detail. To attempt a complete survey of a group containing as many described species as all the known mammals—both recent and fossil—would be to write a book, and probably to obscure the subject. The general phylogenetic relations of the different groups and a simplified epitome of their geological history are shown on Plate 1.

Malacologists are rather generally agreed that the archetypal stock of all of the Mollusca could not have differed greatly from the synthetic form which E. Ray Lankester constructed many years ago, and such a form is shown in longitudinal section in Plate 2, figure 1, in which the shell, visceral cone, course of the alimentary canal, and crawling foot are differentiated. Such a form might readily give origin to gastropod, scaphopod, lamellibranch, or amphineuron. To become an incipient cephalopod it would have merely to narrow the aperture of the shell, heighten the cone, and cut off its apex by septa. How this came about I shall consider presently.

At this point it is necessary to correct another misconception of the soft parts. When the short body of the pearly Nautilus is compared with that of a more active squid the proportions are in striking contrast, and it has been tacitly assumed that the extinct shelled species had bodily proportions comparable to those of the Nautilus. Many had, or were even shorter; others had not, and were quite as elongated as a squid or even longer. Examples can be cited at almost any time during geological history. For instance, the cigar-shaped body of the immature *Proterocameroceras brainerdi* (Whitfield) of the Ordovician was eight or nine times as long as it was wide.

Other early nautiloids with elongated bodies were the genera *Ophidioceras* (fig. 13), *Schroederoceras* (fig. 12), *Deltoceras*, *Piloceras*, *Vaginoceras*, *Lituites*, etc. Among the later ammonoids the genus *Macro-*

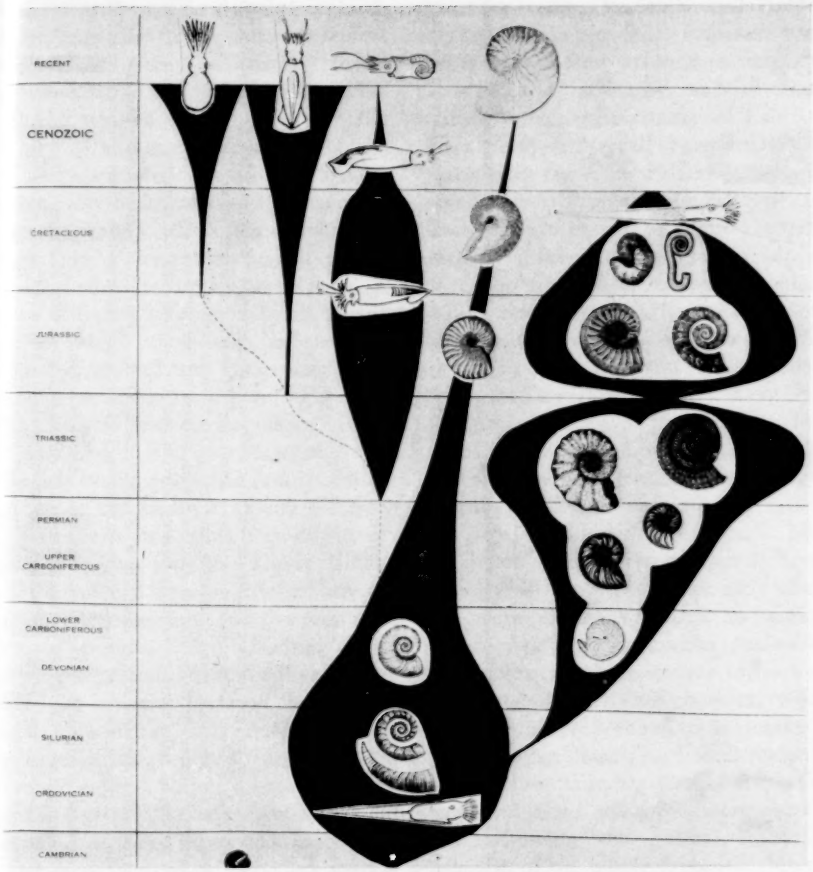


DIAGRAM ILLUSTRATING THE PHYLOGENETIC RELATIONSHIPS OF THE VARIOUS CEPHALOPOD TYPES, THEIR RANGE IN TIME, AND RELATIVE REPRESENTATION IN THE PAST

At the left is the life-line of the relatively modern Octopoda; the next life-line is that of the somewhat more ancient and less specialized Decapoda; the next is that of the Belemnoidea, which reached their maximum during the Mesozoic and are represented in existing seas by *Spirula;* the next is that of the Nautiloidea, which reached their maximum in the earlier Paleozoic. The right hand life-line is that of the Ammonoidea, which appeared in the record in the late Silurian, reached an early maximum of differentiation in the Triassic, became nearly extinct in the late Triassic, rapidly attained a second maximum in the Jurassic and became extinct with the Upper Cretaceous.

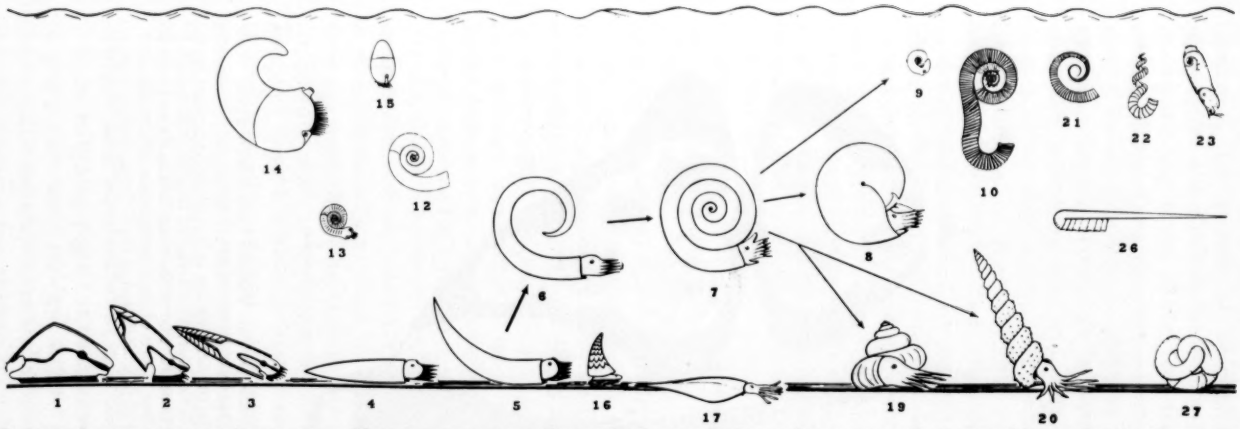


DIAGRAM ILLUSTRATING THE ADAPTATIONAL MODIFICATIONS OF THE CEPHALOPODA WITH EXTERNAL SHELLS, TO BE READ FROM LEFT TO RIGHT. BENTHONIC FORMS AT THE BOTTOM, NECTONIC FORMS IN THE MIDDLE, AND PELAGIC FORMS AT THE TOP

FIG. 1. The Molluscan archetype, hypothetical. (After Lankester.)
FIG. 2. Elongation and contraction of cone, partial transformation of the foot, hypothetical.
FIG. 3. More advanced stage of preceding, hypothetical.
FIG. 4. Horizontal Orthoceras stage.
FIG. 5. Cyrtoceras stage.
FIG. 6. Gyroceras stage.
FIG. 7. Fully coiled stage.
FIG. 8. Involutely coiled stage.
FIG. 9. *Morphoceras pseudoanceps* Douvillé, a pelagic Jurassic ammonite with partially closed aperture. (Bajocian of France, after Douvillé.)
FIG. 10. *Macroscaphites ivani* (d'Orbigny), a Lower Cretaceous non-swimming ammonite. (Barremian of France, after d'Orbigny.)
FIG. 12. *Schroederoceras eatoni* Whitfield, an Ordovician partially floating nautiloid. (Fort Cassin beds of New York, after Ruedemann.)
FIG. 13. *Ophioceras simplex* Barrande, a Silurian partially floating nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
FIG. 14. *Phragmoceras inflexum* Hedström, an endogastric prevailingly floating Silurian nautiloid with constricted aperture. (Silurian of Gotland, after Hedström.)
FIG. 15. *Mandaloceras bohemicum* (Barrande), a pelagic Silurian nautiloid with constricted aperture. (Étage E of Bohemia, after Barrande.)
FIG. 16. *Cyrtoceras parvulum* Barrande, a representative of the breviconic small forms which retained the primitive crawling foot as late as Silurian time. (Étage E of Bohemia, after Barrande.)
FIG. 17. *Gonioceras*, representing a group of greatly depressed benthonic crawlers. (After Ruedemann.)
FIG. 19. *Turrilites robertianus* d'Orbigny, a Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
FIG. 20. *Turrilites tuberculatus* Bosc. Another late Lower Cretaceous benthonic crawler. (Albian of France, after d'Orbigny.)
FIG. 21. *Spiroceras bifurcatum* (Quensted), a Jurassic feebly swimming and floating ammonite (Callovian of Würtemberg, after Quensted.)
FIG. 22. *Heteroceras reussianum* d'Orbigny, an Upper Cretaceous pelagic ammonite. (Emscherian of Germany, after E. Fraas.)
FIG. 23. *Spirula australis* Lamarck, floating position. (After Chun.)
FIG. 26. *Ptychoceras pugosianus* d'Orb., a Lower Cretaceous swimmer. (Neocomian of France, after d'Orbigny.)

scaphites (fig. 10), the family Lytoceratidae, and numerous others, show a similar elongation of the body chamber.

Without attempting a detailed explanation, it may be noted that in either swimming or passively floating forms there seems to be a direct correlation between the weight of the body and the buoyancy of the empty chambers of the shell, calculated to maintain the animal in a normally functional position according to its habits. This may seem like reasoning in a circle, but I shall try to show in a few selected cases that it is not.

Plate 2, figure 2 shows a hypothetical stage in which the shell had become partially elongated and contracted, the visceral cone was correspondingly narrowed, and a few partial septa, lined internally with horny endocones, had developed, much as in the family Endoceratidae of the Ordovician and Silurian periods, though not in such an advanced manner as in that family. The shell had not yet developed enough air chambers to be appreciably buoyant, and the foot had shortened progressively, although still possessing a partially functional crawling surface; its anterior portion had commenced to encircle the mouth, and to assume tactile and prehensile functions.

Plate 2, figure 3 shows a second, more advanced hypothetical stage, with a still narrower and more elongated shell and visceral cone, and more numerous septa. The foot is almost entirely transformed into tentacular segments, which completely encircle the mouth; its hinder portion has the two reduced lateral halves appressed, much as in the taxodont genus *Nucula*, and this part becomes the incipient swimming siphon or hyponomic funnel.

In Plate 2, figure 4 we pass from the hypothetical to the actually observed Orthoceras form with which it is customary to start cephalopod phylogeny. The most obvious feature, giving its name to this type, is that the shell is an orthocone, or straight cone. However, a more searching study of the orthocones that are so abundant in the older Paleozoic rocks shows the greatest amount of variety in the details of structure, and is clearly indicative of a like variety of habits of life. When we recall that orthocones swarmed in the older Paleozoic seas, and largely filled the rôle of the fishes of later times, we are bound to admit the probability of their having become adapted for every possible environmental niche. Some were sluggish, others active; some were benthonic, crawling on the sea bottom; others nectonic or swimming forms; and still others may have been planktonic, floating on the surface. They ranged in size from that of a lead-pencil to giant forms a dozen feet or more in length. (Certain species of *Endoceras* are said to have attained a length of 15 feet.) Their siphuncles were tiny to excessively large, and variously modified; their early chambers were empty or filled to various degrees with organic deposits; some fashioned accessory chambers far forward on top of the adult living chamber, whose buoyancy enabled them to maintain an even keel (See Plate 3). I shall return to some of these modifications of the orthocones and their probable interpretation after following the general course of evolution of the whole group on through to the attainment of the enrolled shells so typical of the late Paleozoic and succeeding Mesozoic era.

PROGRESSIVE COILING OF THE SHELL

If one single feature may be said to characterize the phylogeny of the shelled cephalopods as a whole, it is that of progressive coiling. The older naturalists found a supposed reason for this in the phrase "natural selection favored the

compactly coiled shell," but as Dunbar has pointed out, this explanation, like so many of the natural selection sort of explanations, fails to explain why, or to take into account the intermediate curved (cyrtocone) and incipiently coiled (gyrocone) stages, and this same author, adopting Buckman's idea (1919), has elaborated the true reason, namely: that progressive coiling is an adjustment to the buoyancy of the empty chambers of the shell which induced it.

The older naturalists, commencing I believe with Buckland in 1835, believed that the early chambers of the shell served for hydrostatic purposes, a belief due in the first instance to one of the few mistakes in the account of the anatomy of *Nautilus* given by Owen, who described the axial canal of the siphon as forming a communicating conduit between the empty chambers and the mantle cavity. When the animal wished to descend, these chambers were filled with water; when it wished to rise they were emptied—exactly on the operative principle of a submarine. This idea is perpetuated in the last edition of Eastman's Zittel (1913, p. 589), although Dean's (1901) observations on the identical buoyancy in the living and dead Nautilus and Willey's (1902) demonstration that the siphon does not communicate with the mantle cavity in *Nautilus* should set at rest the hydrostatic myth. The empty chambers in *Nautilus* are buoyant once for all, and what is true in this respect for *Nautilus* should apply to all of the extinct camerated forms that did not fill the early chambers with organic deposits.

This buoyancy of the unfilled earlier chambers is the keynote to the observed changes in shell form, in both phylogeny and ontogeny, and the merit of first applying it in any detail belongs to Dunbar (1924).

With the formation of complete septa shutting off the apical chambers in the developing orthocones, their buoyancy in those forms that did not weight this end by organic deposits filling the chambers or elaborate deposits about the enlarged siphuncle would tend to tilt the shell forward. Such a tilting would be a handicap in either a nectonic or benthonic animal. Whether the resulting tension on the ventral side would cause a more rapid growth of the ventral shell margin, or whether normal secretion of the animal in so orienting its body as to keep its mouth out of the mud of the bottom or to remain horizontal in the water would be the predominant factor cannot be decided. In any event, the more rapid growth on the ventral side would result in an arcuate shell—the cyrtocone (Plate 2, fig. 5), and the more the curvature, the more the forward migration of the center of gravity would be retarded.

This finally resulted in the gyrocone type of shell (Plate 2, fig. 6). The progressive coiling would not stop with this type since, as the shell is an expanding cone, the newest chambers immediately behind the living chamber, with their exterior position and much increased volume, would throughout adolescence tend to tilt the animal forward, and this would eventually result in the coiled type of shell known as an ophiocone (Plate 2, fig. 7). Complete equilibrium with the animal in a horizontal position most effective for swimming is only attained when the later chambers entirely invest the earlier whorls as in the existing *Nautilus pompilius*, a completely involute form. Or an ophiocone may attain the same stability if there are many volutions to the shell, which serves to explain the persistency of the latter type.

The foregoing simplified series of stages, illustrated by figures 1–8 of Plate 2, is

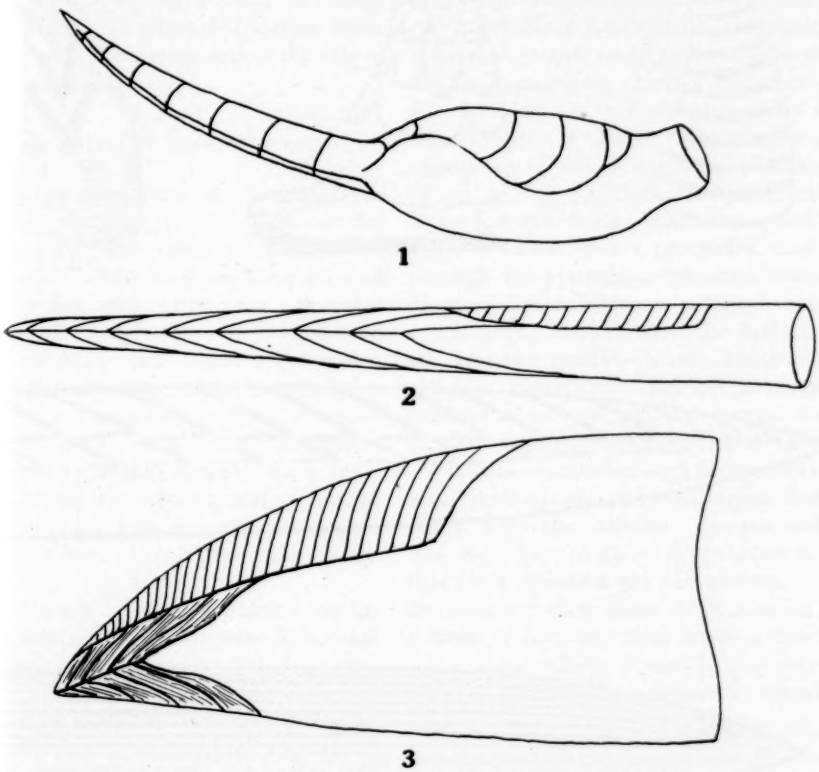
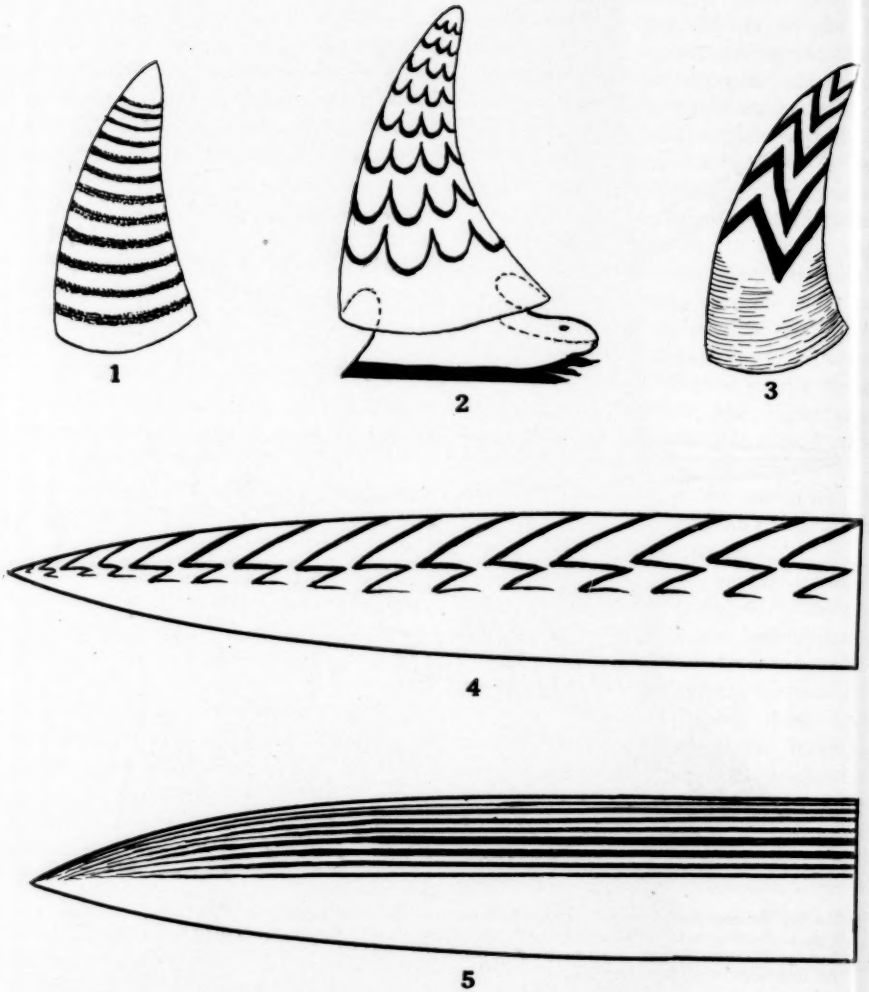


FIG. 1. *Ascoceras*, based upon *Ascoceras bohemicum* Barrande, from the Silurian of Bohemia.
FIG. 2. *Proterocameroceras brainerdi* (Whitfield). Ordovician of New York. (After Ruedemann.)
FIG. 3. *Piloceras*. (After restoration by Ruedemann.) An Ordovician type.
All in median longitudinal section.



COLOR PATTERN AND ATTITUDE AMONG THE EARLY NAUTILOIDS

FIG. 1. *Cyrtoceras fallax* Barrande. Silurian of Bohemia.
FIG. 2. *Cyrtoceras parvulum* Barrande, showing color pattern and restoration of soft parts. Silurian of Bohemia.
FIG. 3. *Cyrtoceras decurio* Barrande. Silurian of Bohemia.
FIG. 4. *Orthoceras anguliferum*. Middle Devonian of Germany. (After Dunbar.)
FIG. 5. *Geisonoceras tenuitextum* (Hall). Middle Ordovician of New York. (After Ruedemann.)

an epitome of the general and normal trend of evolution in the shelled cephalopods. The end product would be a nectonic animal with greater or less locomotive powers—as were the majority of shelled forms. But there are a host of exceptions to this general trend, as there necessarily must have been if these animals were to adapt themselves fully to the varying environments of the seas—as they undoubtedly did.

LIFE HABITS OF THE ORTHOCONES

In considering these modifications we may first consider the variations shown in the early orthocones. Fully half of the known Ordovician cephalopods had shells which were orthocones. Speculations as to their habits of life have been more fantastic and mutually exclusive than is the case in any of the later cephalopods. They have been pictured as swimming in both vertical and horizontal attitudes, as having dragged their horizontal shells over the bottom, as having lived obliquely buried in the bottom, or as having been attached vertically by the apical end.

Ruedemann (1921) has shown conclusively that some of them were horizontal in their normal attitude. This is proved in the case of *Geisonoceras tenuitextum* of the Ordovician of New York by the preservation of a well marked longitudinal color pattern (Plate 4, fig. 5) on one side of the shell, which must have been the dorsal, since all marine organisms with a color pattern have the side toward the light contrasted with the opposite side. Not only so, but this author cites shells of this species with incrusting bryozoa in which the zoarium begins near the apex and extends forward on one side of the shell only, *pari passu* with its growth, which would be a most unlikely occurrence if the bryozoan had started on a dead shell.

If this dorso-ventral color pattern were an isolated case it might possibly be open to doubt, but it has been observed in specimens of orthocones of very different ages and widely separated geographically. Naturally the preservation of the color pattern of life in fossils of great antiquity is unusual, so that many such instances are not to be expected. Nevertheless I may cite such features in *Orthoceras trusitum* of the Silurian of New York, *Orthoceras anguliferum* of the Devonian of Germany (Plate 4, fig. 4), *Orthoceras* sp., of the Upper Carboniferous of Oklahoma, and I have no doubt that a protracted search through the systematic literature would disclose other instances. Those cited extend pretty well through the Paleozoic and over two continents, and I think that we may legitimately conclude that the horizontal attitude was the normal one for the majority of the orthocones.

Ruedemann considers such forms to have been benthonic and to have dragged their shells over the Paleozoic sea-bottoms. The objections to this interpretation are that their apertures are not oblique, the shells do not show wear incident to such a mode of life, and many show a hyponomic sinus which is usually correlated with a functional hyponomic funnel.

This last is not an especially weighty objection, since all cephalopods must have preserved the funnel for respiratory purposes even when it ceased to be functional as a locomotive organ; at least in the modern Nautilus its regular pulsation causes incurrent and excurrent streams, and the mantle does not take part in causing these movements, as it does in the dibranchiates.

I believe such forms to have been swimmers. Some doubtless hovered near the bottom or spent most of their time resting upon it, but others surely must have been more active. The idea that locomotion

backward was awkward is wholly anthropomorphic—it is to us, but is decidedly not for a cephalopod. The other idea that they would run the risk of fracturing the apex of the shell is altogether fanciful —they did not find their optimum conditions of life on a stern and rock-bound coast, and in any event nature usually provides against accidents in its tendency to overpopulation. (Pathological rostra of the Mesozoic belemnites are found fossil.)

Many students can not dismiss the idea from their minds that the cephalopod shells were too heavy and too unwieldy to have been propelled by the relatively simple method in vogue among these animals. This rests almost entirely upon the handling of museum specimens in which the chambers are filled with sediments, lithified, or calcified, or impregnated, or replaced with marcasite, etc. In the vast majority of forms throughout their whole geologic history, the shells were thin and in life were relatively light and easily propelled, and the specific gravity of the whole animal was close to that of the medium—so close, I imagine, that when the animal was expanded to its maximum extent it would float or rise in the water, and when withdrawn within its living chamber it would sink.

A belief in the swimming habits of the majority of orthoconic forms is also a reason for regarding them as having had "arms" like a squid rather than tentacles like a Nautilus, since when swimming these would trail behind, as do the extended tentacles in the Nautilus, and would furnish the necessary rudder to guide their passage through the water more effectively than tentacles. Obviously not all orthoconic forms were swimmers. I would expect such swimming forms to show some compression in the cross profile of the shell, and this is perhaps true in a majority of cases. Crawling or grovelling forms should show some depression in the cross profile of the shell, and this can be seen in a number of forms.

The extreme example of depressed shell form, undoubtedly indicating a sedentary bottom-dwelling animal, which had probably lost the swimming habit and could move only by dragging its shell by the use of its arms, is the genus *Gonioceras* (Hall, 1847). This includes five or six Ordovician species found in Ontario, New York, Illinois, Wisconsin, Minnesota, and northern China. The shell is several times as wide as it is high, with lateral flanges; the septa are closely spaced and sinuous; and the siphuncle is large and nummuloidal. At maturity the aperture is greatly constricted. Since the muscular attachment of the animal to its shell is not especially firm throughout the Cephalopoda, this constriction of the aperture in *Gonioceras* would serve to prevent the rupture of the muscular attachment when the shell was pulled along over the bottom, and the angularity of the septa would also serve to give the animal a firmer hold on its shell. Hyatt (1884 and 1900) made some wild guesses regarding the affinity of this curious form; we are not, however, at present concerned with its taxonomic position, but only with its obvious adaptation to a benthonic existence; from this point of view it is completely adapted, and ceases to be curious—the large nummuloidal siphuncle may be regarded as ballast, helpful in maintaining an even keel (Plate 2, fig. 17).

I have already mentioned the habit of some of the earlier orthocones of using the siphuncle in this way, or of filling the earlier chambers to a greater or less degree with organic deposits to counteract their buoyancy. Large and often elaborately ornamented siphuncles occur in a number of families of nautiloids, as for example in the families Endoceratidae, Pilo-

ceratidae, and Cyrtendoceratidae; and every degree of internal filling of the earlier chambers may be seen in the families Actinoceratidae, Jovellanidae, and Poteriocerati dae—collectively covering the time from Ordovician to Devonian.

An equally effective method of maintaining horizontality is illustrated by the families Ascoceratidae and Mesoceratidae —constituting the sub-order Mixochoanites of Hyatt—Ordovician and Silurian nautiloids. In these the shells have advanced slightly beyond the orthoconic form in most of the genera and are more or less cyrtoconic. The living chamber of the adult is long and inflated, often contracted at the aperture, which is sometimes crested. The manner in which the center of gravity is kept back is by the formation of a linear series of air chambers (saddles) along the dorsal wall of the living chamber. Two examples of this are shown in the accompanying figures (Plate 3): *Proterocameroceras*—an orthoconic form, and *Ascoceras*—a cyrtoconic form. A somewhat similar arrangement is exhibited in the allied family Piloceratidae of the Ordovician. In *Piloceras* the shell is relatively short and wide; the animal was stout, its visceral cone extending backward over six-sevenths of the distance to the apex of the shell; the living chamber is restricted dorsally and the animal thus rendered buoyant by the development of numerous dorsal saddles (air chambers), and the apex of the shell is ballasted by pseudosepta and conchyolin endocones.

According to Geikie, (I have not taken the pains to verify his count) the Silurian of the Bohemian basin furnished Barrande with 1127 species of Cephalopoda. Of these 554 were orthocones, and other statistically minded students have estimated the number of orthocones in the Ordovician as approximately fifty per cent of the total number of species of Cephalopoda known from that period. The percentage is somewhat less for the Silurian as a whole, about 25 per cent for the Devonian, and about 20 per cent for the Carboniferous as a whole, although some very large sized forms do survive as late as Carboniferous times. In post Triassic times there are no orthoconic nautiloids. This proves that the general course of evolution in this sub-class was as I have indicated, and effectually combats the seemingly eccentric view of Owen —in which strangely enough he is followed by Willey and Spath—that the orthoconic are uncoiled from whorled ancestors.

THE CYRTOCONES

The number of species of cyrtocones in the Silurian of the Bohemian basin was 330. Both orthocones and cyrtocones were all originally referred to the two comprehensive genera *Orthoceras* and *Cyrtoceras*, but later systematists have partially segregated them into more natural generic groups. I have already indicated a probable variety of habits among the orthocones, and this is quite as clearly indicated among the cyrtocones. There can be slight doubt that what might be called the normal cyrtocone was derived from orthoconic ancestors in the manner already outlined, or that such a one as is shown in Plate 2, figure 5 was a horizontal swimmer.

Among the cyrtocones, however, there are a considerable number of so-called breviconic forms, all from the Silurian (Étage E), which it seems to me throw an important light on their structure and habits. They are all of about the same size, i.e. 4 to 5 centimeters long and 2 to 3.5 centimeters in maximum diameter, and hence justly called small forms, and are conspicuously marked by mostly transverse color patterns that entirely encircle the shell and prove conclusively

that these shells were held erect in life and equally illuminated on all sides. By the same token the animals were benthonic crawlers and not swimmers. Not only were they crawlers, but I believe that they crawled by means of a soled foot like that of a gastropod and not by means of their tentacles as does the existing octopus. In fact, were it not for their camerated shells and siphuncles one would be disposed to doubt their cephalopod character and consider them gastropods.

My restoration of *Cyrtoceras parvulum* Barrande will indicate sufficiently my conception of the animal (Plate 4). The extent to which the soled foot has assumed a tentacular form in front is, of course, entirely problematic. If these forms were organized as I have assumed, they would represent a survival, as late as the Silurian, through a continuous ancestry, of the primitive nautiloid organization of the early Cambrian or pre-Cambrian, and would be otherwise unrelated to their contemporary cyrtoceran associates.

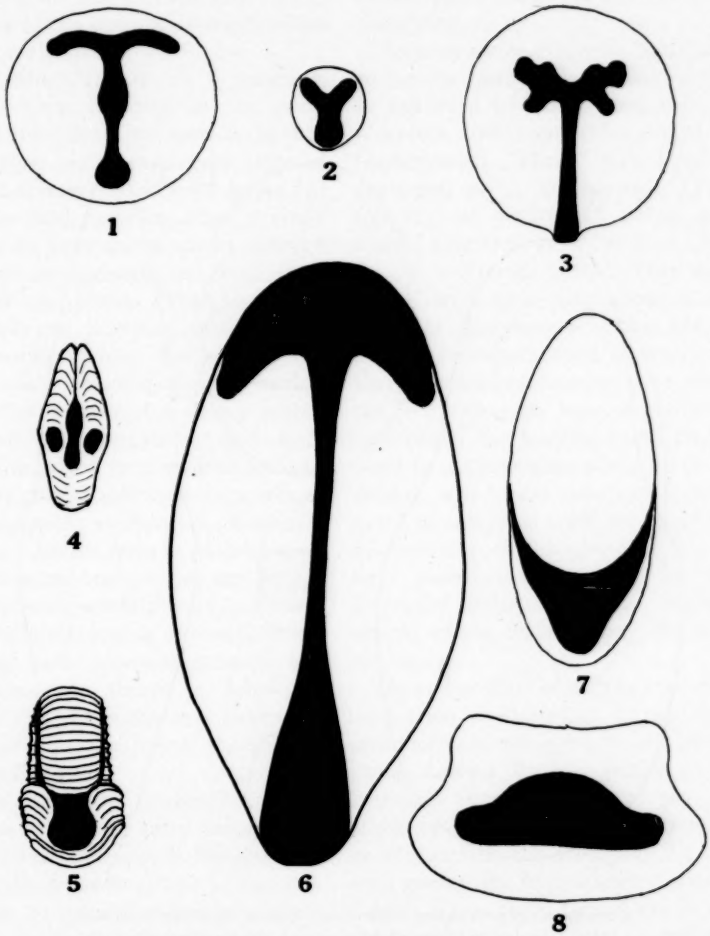
Among these cyrtocones with color patterns on all sides of the shell are *Cyrtoceras fallax* Barrande, with straight transverse bands; *Cyrtoceras zebra* Barrande, with closely spaced fine subparallel wavy bands; *Cyrtoceras intricans* Barrande, with somewhat more angular and less regular bands, more pointed backward than forward and perhaps prenuncial to chevrons; *Cyrtoceras veteranum* Barrande, with closely spaced chevrons; and *Cyrtoceras decurio* Barrande with large angular chevrons. A sixth species is ornamented with spots all around.

ADAPTATIONS FOR A MORE OR LESS PASSIVELY FLOATING MODE OF LIFE

Adaptations by means of which the animal spent most of its existence in passively floating are various and are attained in unrelated stocks throughout the geological history of the class. Whether they floated near the surface, in intermediate depths, or hanging over the bottom—the feeding ground of the existing Nautilus—is immaterial; certainly those forms which retained locomotive powers could readily maintain their position at any desired depth. In the adaptation diagram (Plate 2) all floating forms have been placed near the surface, but this is solely a matter of composition on a crowded diagram. The recurved aperture in such an ammonite as *Macroscaphites*, or in some species of *Heteroceras* or *Nostoceras* leads to the conclusion that they drifted over the bottom while feeding, but in other genera there is no definite evidence on this point.

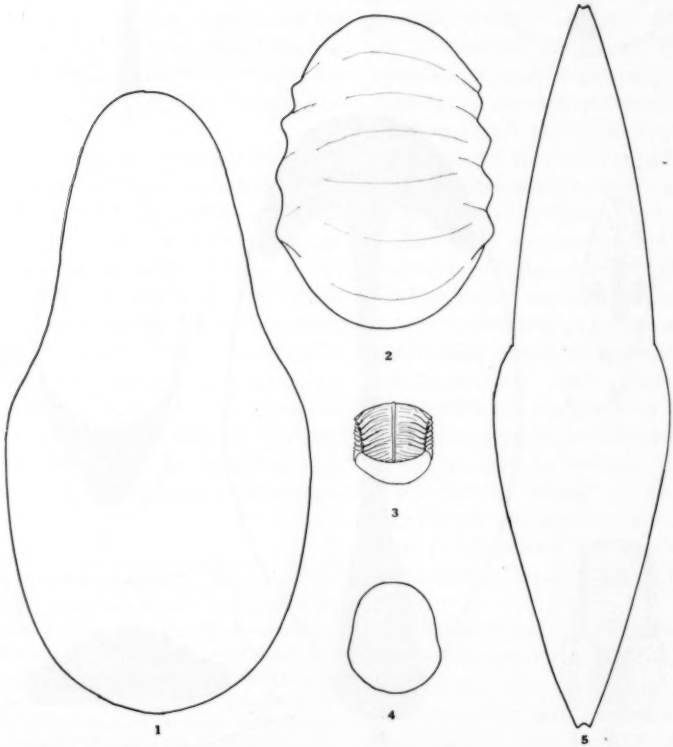
There are a considerable number of orthoconic Nautiloidea, prevailingly small and breviconic, found from the Ordovician to the Carboniferous, and principally in the families Rizoceratidae, Oncoceratidae, Poterioceratidae, and Trimeroceratidae, represented by a variety of genera, and exhibiting numerous differences in their structural details, which floated head downward by reason of the gas filled chambers of the apex of the cone. This type is illustrated in the diagram by *Mandaloceras* (Plate 2, fig. 15), a Silurian genus.

In *Mandaloceras* this position must have been maintained from infancy onward. At maturity the aperture of the living chamber was greatly contracted, but the hyponomic funnel probably retained its propulsive powers, since the space in front of it was not roofed over by the inflected margins of the aperture. The expulsion of water from the mantle cavity through the funnel would cause the animal to rise vertically. Many other of these forms had variously contracted apertures leaving only restricted openings for the eyes, tentacles, mouth, and funnel. Many students have thought that this was to be interpreted as indicating that their food



VIEWS OF VARIOUSLY CONSTRICTED APERTURES, ALL NATURAL SIZE

FIG. 1. *Mandaloceras bohemicum* (Barrande). Silurian of Bohemia.
FIG. 2. *Ophioceras simplex* Barrande. Silurian of Bohemia.
FIG. 3. *Tetrameroceras panderi* (Barrande). Silurian of Bohemia.
FIG. 4. *Morphoceras pseudoanceps* Douvillé. Bajocian of France.
FIG. 5. *Normannites braikenridgei* (Sowerby). Middle Jurassic of France.
FIG. 6. *Phragmoceras inflexum* Hedström. Silurian of Gotland.
FIG. 7. *Arcestes intuslabiatus* Mojs. Upper Triassic of Austria.
FIG. 8. *Hercoceras mirum* Barrande. Devonian of Bohemia.



END PROFILES OF VARIOUS CEPHALOPOD SHELLS, REDUCED ONE-HALF

FIG. 1. *Nautilus pompilius* Linné, the best known existing species of *Nautilus*.
FIG. 2. *Polyptychites laticosta* von Koenen. Neocomian of Germany. (After von Koenen.)
FIG. 3. *Tropites subbullatus* (Hauer). Upper Triassic of Austria. (After Hauer.)
FIG. 4. *Cyclolobus stachei* Gemmellaro. Late Paleozoic of Sicily. (After Gemmellaro.)
FIG. 5. *Placenticeras meeki* Boehm. Upper Cretaceous of South Dakota.

was microscopic, and Abel has dubbed such forms microphagous. I see no reason for limiting the size of their food except by the size of the opening through which it had to pass (Plate 5).

The existing Nautilus is a voracious carnivore, very catholic in its taste. Doubtless the size of the aperture in such a fossil form as *Mandaloceras* imposed somewhat narrow limits with respect to size of the food particles, since it could not excert its jaws and tentacles through so narrow an opening and tear large sized prey to pieces. The contracted aperture was not, however, an adaptation due to feeding habits, but exactly the opposite, the contracted aperture having originated as a protective device which also served to keep the animal from becoming dislodged from its living chamber, exactly comparable with the apertures in such land snails as *Polygyra*, *Anastomia*, and *Pythia*. Such a form as *Mandaloceras*, if its aperture had been an open one, would have been a juicy morsel for its larger and more actively swimming contemporaries, and to call such apertures gerontic features is about as absurd as Schmidt's suggestion that the young may have been protected within the living chamber of the mother by them.

Many of these early floaters had shells which were cyrtocones, often endogastric, as in the Silurian nautiloid *Phragmoceras*, shown in the diagram (Plate 2, fig. 14). These were in general somewhat larger forms than the breviconic orthocones like *Mandaloceras*, but like them they retained the functional hyponomic funnel, and had greatly constricted apertures during their adult life. What was said of *Mandaloceras* applies also to forms like *Phragmoceras*, except that the latter could probably propel themselves horizontally. To rise or sink they would have to depend on the extension or contraction of the arms to induce changes in their specific gravity, unless, like the existing *Spirula*, they could point their funnel in different directions.

Another series of evolutionary changes in the direction of adaptations for floating is exhibited by those nautiloids whose ancestors had completely coiled shells (ophiocones). These may have open apertures, as in *Schroederoceras* (Plate 2, fig. 12), an Ordovician genus; or contracted apertures, as in *Ophioceras* (Plate 5, fig. 2), a Silurian genus. They are contrasted with such adaptations as *Mandaloceras* or *Phragmoceras* in that they were normal swimmers with normally coiled shells during adolescence. At maturity the living chamber became partially free (uncoiled), the margins being built outward to accommodate the growth of the animal, which was then strikingly elongated as compared with the short bodied *Mandaloceras* or *Phragmoceras*, and must have passed the remainder of its life suspended obliquely in the water—the weight of the body causing the shell to tilt forward.

The end product of such an evolutionary adaptation as *Ophioceras*, in which it is prenuncial, is exhibited by the nautiloid genus *Lituites* Breyn., which in early Paleozoic time (Ordovician) set an example of modification that was repeated in substantially the same way by ammonoid genera like *Macroscaphites*, eons later. *Lituites* was a fairly large form in which the first three whorls form an ophiocone, indicative of its ophioconic ancestry, as well as its normal swimming attitude during adolescence. After this stage of its ontogeny the diameter of the shell increases rapidly and it is nearly straight in its growth for a distance about 14 times the diameter of the coiled early portion. The aperture has a shallow hyponomic sinus, narrow ventro-lateral crests, broad

lateral sinuses, and fairly well developed dorso-lateral crests. The living chamber was extraordinarily long, and the consequent weight of the animal must have caused the shell to assume an almost vertical attitude in the water. The adult Lituites must have drifted, head down, picking up its food on or near the bottom. If the hyponomic funnel remained functional, as the presence of a hyponomic sinus would seem to indicate, it would serve to propel the animal upward, which would then sink slowly. A very slight action of the funnel would serve to keep the animal at any favorable horizon where food happened to be abundant.

Among the ammonoids floating adaptations are expressed in various ways. Least modified are various genera of the family Stephanoceratidae, such as *Normannites* Munier-Chalmas of the middle Jurassic, in which the aperture is so contracted (Plate 5, fig. 5) that it is difficult to visualize a functional hyponomic funnel, although this is not impossible. Another involutely coiled small form which seems to have been pelagic is the genus *Morphoceras* Douvillé (Plate 2, fig. 9) of the Jurassic and Cretaceous, in which the adult aperture was almost entirely closed and swimming would seem to have been precluded (Plate 5, fig. 4). I have pictured it as planktonic.

Modified in a different way are those forms which were tightly coiled in their youth, but which have the very long adult living chamber suspended, and frequently recurved near the aperture. A good example of this adaptation is furnished by the Lower Cretaceous genus *Macroscaphites* Meek (Plate 2, fig. 10), which, like the Ordovician nautiloid *Lituites*, must have been a swimmer in its youth. At maturity the body chamber hangs down for a distance about equal to the diameter of the coiled disk and finally curves upward at its lower end. I consider *Macroscaphites* to have normally drifted, foraging over the bottom, the position of the aperture raising the head above the bottom in an advantageous manner. Possibly the specific gravity was so adjusted that the shell would sink when the animal was withdrawn within the living chamber, and rise when it was extended; or when extended and foraging the funnel, by its action, might either reinforce the induced buoyancy or tilt the hook-shaped distal end of the shell so that the animal had no difficulty in seizing its prey on the bottom.

The genus *Hamites* Parkinson, of the Cretaceous, functioned exactly as did *Macroscaphites*, only in the former genus the early shell was not tightly coiled but was a gyrocone. All of the members of the sub-family Scaphitinae, as exemplified by the genus *Scaphites* Parkinson, a world-wide Cretaceous type, were more or less floaters. Indeed it is difficult to see how the adult of such a species as the Cenomanian *Scaphites aequalis* Sowerby could have swum at all. On the other hand it is readily conceivable that a form with the aperture oriented as in *Scaphites spiniger* Schluter—a German Upper Cretaceous species—might well have been able to swim.

Still another type is illustrated by such genera as *Spiroceras* Quenstedt of the Jurassic (Plate 2, fig. 21), or *Crioceras* Leveillé and *Ancyloceras* d'Orbigny, of the Cretaceous. In these the shell is a gyrocone, and such a type might well be a form leading in the direction of *Hamites* (supra). Another form that appears to me to indicate a floating existence is such a species of *Heteroceras* as *Heteroceras reussianum* d'Orbigny (Plate 2, fig. 22) from the Upper Cretaceous of Germany. This was relatively a small form with a

shell coiled in an open ascending spiral, its apertural end recurved as in *Macroscaphites*, and, I believe, had from infancy the habits described above for the mature Macroscaphites. The genus *Heteroceras* of d'Orbigny is confined to the Cretaceous period, and all of its species have trochoid spiral shells, but many tend to irregularity, and some appear to have been benthonic crawlers rather than pelagic. Such a form as *Heteroceras stevensoni* appears to me to have had a crawling rather than a swimming or floating habit.

Such genera as *Hamulina* d'Orbigny and *Ptychoceras* d'Orbigny of the older Cretaceous appear to include highly anomalous forms. During growth their shells are relatively slender chambered orthocones, and if the earlier chambers contained gas, as there are no reasons for doubting, it is impossible to see how they could have been oriented except head downward. At maturity the shell, now much enlarged, bends through an arc of 180 degrees and continues its growth in the opposite direction, the animal now facing the apex of the shell. This adult enlargement of the body, faced about as it was, would thus shift the center of gravity backward, so that the animal would now be able to swim in a horizontal position, as I have indicated (Plate 2, fig. 26). In some species of *Ptychoceras* the living chamber extends further backward than in the species that I have figured. For example, in the much smaller Neocomian species, *Ptychoceras emericianus* d'Orbigny, it extends three-fourths of the distance toward the apex of the shell.

In the genus *Ptychoceras* the flexed portion is in contact with the earlier part of the shell. *Hamulina* differs merely in that the two parts do not come into juxtaposition. Hyatt and other authors speak of such forms as these partially uncoiled or secondarily straightened ammonites as "degenerate," but they are obviously not degenerate in any way unless one adopts a creed, and considers the closely coiled form of shell the ideal of perfection. Doubtless the last was an ideal for a swimming habit, and that is why such forms predominate in the geological record of the Mesozoic era, but from the point of view of adaptation a Macroscaphites was more specialized, and in its adult form would have avoided a certain amount of competition which it suffered in its youth. If cephalopods, or other organisms, can have imputed to them any purposes other than to live and reproduce their kind, then, and then only, is it permissible to speak of modifications such as these as degenerate.

ADAPTATIONS FOR A CRAWLING BENTHONIC LIFE

In considering the mode of life of the swarming ammonites of the Mesozoic and in endeavoring to find some sort of seemingly rational explanation for their remarkably complicated septa, the older naturalists, noting that the growth lines across the venter and the margin of the aperture, when this was preserved, usually showed no trace of a hyponomic sinus such as is present in the majority of the nautiloids, reasoned that there was no hyponomic funnel, and hence that the ammonites as a group were not swimmers, but crawlers on the bottom by means of their tentacles; and that this habit had induced the development of the lobes and saddles in the septa, since this would enable the animal to hold and balance its shell more effectively while crawling.

This view has been widely accepted, although it is open to insuperable objections. It entirely ignores the meaning of their prevailingly high and often greatly compressed, bilaterally symmetrical, planospiral shells; it ignores the fact that

a hyponomic funnel is essential for respiration; it ignores the universal principle of organisms, namely: that a dominant group tends to utilize all available habitats more or less completely; and it disregards the meaning of the wide geographic range that a number of species show.

Narrow planospiral shells fulfil what might be called the stream-line form for disks. Many, such for example as a large Sphenodiscus, have lines that obviously indicate a movement through the water, and how such high and narrow shells could have been manipulated by a crawling animal is incomprehensible. It is true that there are a number of genera of benthonic gastropods scattered through many families and sub-orders that have planospiral shells. In the planospiral gastropods the shells are generally small and their apertures wide—usually wider than high. None approach the cephalopod shell-form, unless it is the tiny early stage of the genus *Caecum*, so that I think it may be conceded that the normally lenticular form of the coiled Cephalopoda —whether nautiloids or ammonoids—is indicative of a swimming habit.

There are, however, great differences in the transverse profiles of their shells, which doubtless indicate different degrees of resistance to slipping through the water, and in a general way ammonites as a whole are more compressed than nautiloids, the most compressed ammonites, with "cut water" keels or venters, being, in general, among the later forms.

Among the coiled shells of both nautiloids and ammonoids the swimming ability was not only conditioned by the form of the shell and the resistance it offered to passage through the water, but also by the power of the hyponomic funnel, and there is no means of obtaining information on this second factor, since I do not regard the presence or absence of a hyponomic sinus as a reliable indication. This last may perhaps be used with caution, but there are forms—*Placenticeras*, for example—that I regard as active swimmers, but that show no hyponomic sinus.

Transverse profiles of various forms from all horizons show variations from wide ellipticity to extreme compression. The existing Nautilus, which has almost as blunt prowed a shell as can be imagined (Plate 6, fig. 1), a shell certainly wider than in the majority of fossil forms, is known by observation to swim moderately well, which shows how cautiously shell form must be used in predicating locomotive ability. I have shown three more depressed and wider forms in the accompanying illustrations—a *Polyptychites* (Plate 6, fig. 2) from the Lower Cretaceous, a *Tropites* (Plate 6, fig. 3) from the Triassic, and a *Cyclolobus* (Plate 6, fig. 4) from the late Paleozoic, all of which would seem to have been exceedingly poor swimmers. For comparison with these a profile of *Placenticeras*, with what I regard as fast lines, is shown. I believe that all highly compressed forms, and the ammonites show them at all later horizons—*Sageceras* and *Pinacoceras* (*layeri* Hauer) from the Triassic, *Oxynoticeras* from the Jurassic, *Placenticeras* and *Spenodiscus* from the Upper Cretaceous, etc.—were rapid swimmers. Otherwise their shell form is meaningless, and it is impossible to imagine the animal as having been able to handle such high and narrow shells in any other way.

There are shell forms, however, both among Nautiloids and more commonly among the Ammonoids, appearing sporadically throughout all cephalopod history from the Devonian to the Upper Cretaceous, that became secondarily adapted for a benthonic mode of life. All trochoid

shells, unless they can be referred to habits of life such as I inferred for *Heteroceras reussianum* (supra), may be considered to have led a benthonic existence, and their shells, although much less diversified, may legitimately be compared with those exceedingly numerous gastropods whose shell plan is an ascending spiral. Instances of a greater degree of reversed adaptation are furnished by the marine limpet-like pulmonates *Siphonaria* and *Gadinia*, whose ancestors became terrestrial, their descendants of these two genera reentering the sea and becoming benthonic.

That such modifications of the cephalopod shell are not confined to the closing days of ammonite history, but occur also in the Paleozoic nautiloids, is proof that they are adaptations, and not degenerations or phylogerontic features. As I have stated, trochoid shells are far more numerous among ammonoids than among nautiloids; and among the latter are unknown from horizons earlier than the Devonian. This is just what might be expected if cephalopod evolution was anything like I have outlined. Not only did they take their origin from a benthonic stock, but it required long ages to acquire the coiled shell. Even as late as the Devonian 25 per cent of the cephalopods were orthocones and, as has been shown, some of these were benthonic, as were also the breviconic cyrtocones, so that there was no especially untilled field on the sea bottom to tempt the adoption of this mode of life among the nautiloids.

We may also infer from the transverse profiles of the shells, although this is highly problematic, that the nautiloid swimmers as a class were less effective swimmers than the later ammonoids, and fed for the most part near the bottom, as does the existing Nautilus. We may also infer that competition for food was keener among the Mesozoic ammonoids than it was among the Paleozoic nautiloids, or that the food of the latter was more exclusively nectonic, so that there would have been a greater stimulus for the adoption of a benthonic habit in the Mesozoic than in the Paleozoic, although this is very hypothetical. Nor can the influence of the great abundance of mostly benthonic arthropods in the older Paleozoic (trilobites and meristomes), or of the arthrodiran, ostracoderm, and true fishes, be ignored in seeking an evaluation; but the influence of these factors, important as they are, is so obscure that I will not attempt to discuss them.

A secondarily benthonic nautiloid, descended from a coiled swimming ancestor is the Devonian genus *Trochoceras* Barrande. Among the ammonoids the small Cochloceratinae, as exemplified by such genera as *Cochloceras* Hauer, or *Paracochloceras* Mojs., of the marine Triassic, may be mentioned as among the earliest. In the later Mesozoic there are a number of such genera, for example: *Turrilites* Lamarck, *Emperoceras* Hyatt, *Helicoceras* d'Orbigny, and probably some species of *Heteroceras* d'Orbigny—all from rocks of Cretaceous age. The first especially often reaches a large size. Two of these secondarily benthonic ammonoids are shown in the adaptation diagram (Plate 2, figs. 19 and 20). Doubtless the empty early chambers in these forms so reduced their specific gravity that the energy of handling them was reduced to a minimum.

The extreme of benthonic adaptation is that of the apparently sessile, or at least static, genus *Nipponites*, described by Yabe recently from the Upper Cretaceous of Japan, but much fuller information is desirable before attempting to visualize its habits. *Nipponites* was irregularly coiled like some species of *Vermetus* or *Serpula*—a tendency which may be said to

be shown to a very slight degree in species of *Heteroceras* or *Nostoceras*, but which in its extreme development in *Nipponites* is, for the present, highly anomalous. As in the Gastropod genus *Vermetus*, *Nipponites* was undoubtedly derived from a trochoid coiled ancestor.

THE PROBLEM OF SEPTA AND SUTURES

The familiar septal and resulting sutural progression from nautiloid (smooth curves), through goniatitic (angular) and ceratitic (frilled lobes), to ammonitic (frilled or digitate lobes and saddles), is well known, and in a general way is an epitome of the evolution of these parts. It is not, however, a simple linear series. Early forms often show unusual specialization, and later forms simplification, but it is well to avoid the philosophic implications of the terms acceleration and retardation, so much a part of the vocabulary of the cephalopod students of the penultimate generation.

A comparable change from septal simplicity to septal complexity may be observed in the ontogeny of the more evolved types, and this is the basis for the enormous literature on the biogenetic law as exemplified by the shelled cephalopods. It is commonly assumed that the sutural are the most constant features, and that however much the body-form or ornamentation may vary, the court of last resort in determining genetic relationships is the suture, which is said to be constant in species when individuals of the same degree of maturity are compared. This has now become a tradition among students of ammonites, but like all similar traditions, it is unsound, and the only way to establish it would be for systematists to consider every slight variation indicative of distinct species. In an account, shortly to be published, of the ammonite faunas of Peru, a student of mine, M. M. Knechtel, has shown considerable variation of single sutures on the two sides of the shell, and similar features have occasionally been recorded by earlier workers. In such a case the dogmatist must either admit sutural variation or contend that the two halves of the same shell belong to different species.

It is not my purpose in this essay to go deeply into this vexed question, with all its implications, but it may be stated as a general principle that the taxonomic value of such features as sutural pattern, shell form, ornamentation, etc., will vary greatly from genus to genus. In some cases one and in other cases another feature will be entitled to the greatest weight, but there will be no single magical criterion.

The factors that led to the increasing complexity of septa in the ammonoids have been a favorite field for speculation since von Buch first emphasized its existence by proposing the so-called genera *Goniatites*, *Ceratites*, and *Ammonites*. The subject remains obscure to the present, and none of the suggestions that I have encountered seem satisfactory. That it is related in some way to habit would seem probable by the essentially goniatitic form of the sutures in such a nautiloid as *Aturia*, which every beginner thinks is an ammonite; but that benthonic forms can be distinguished from planktonic or nectonic by the characters of the sutures, as Schmidt implies in a recent paper, or that Keferstein's wholly hypothetical "preseptal gas" shows that animals with highly complicated sutures were divers, is wholly without foundation.

In a way progressive sutural complexity is to be correlated with increase in bodily size in excess of increase in shell capacity. This is also a factor in the corresponding sutural modification during ontogeny, for

I do not believe that all of the blame can be fastened upon the hereditary genes. Also, and more clearly, it is to be correlated with a more secure connection between the animal and its shell. This is to be rather conclusively inferred from the complementary relationship between the degree of development of adjacent lobes and saddles, where highly modified laterals tend to bring about underdevelopment in their fellows.

We are now fairly familiar with the formation of the septa in the existing Nautilus, which have their inception in the epidermis of the hind part of the visceral sac; this first becomes a membrane, is then conchyolinized, and finally calcified from the periphery inward on its anterior side next the animal. Hence the horny nidus is left behind the calcified septum. That septa are formed periodically, and alternately with periods of active metabolism, is inferred from their general regularity of spacing and from the correlation between growth lines of the shell and the spacing of the septa, as is shown, for instance, in Ruedemann's description of the shell of an Ordovician species of *Geisonoceras*.

It was long supposed that the flaccidity following the expulsion of the sexual products marked the time of septal formation, but as Willey has shown in *Nautilus*—and I think that his observation may be used for generalization—the last septum is formed before puberty. Perhaps septal formation may be correlated with seasonal climatic change, either as a direct factor or through the influence of climatic change upon food supply, although it must be admitted that seasonal climatic variations are minimized in the seas.

If snakes had shells, the annually shed skins would be accumulated in such a shell exactly (homologously) as are the endocones of the early Endoceratidae, and we may visualize in this periodic shedding of the hardened skin of the apical cone in the earliest nautiloids the beginnings of septal formation. If the extinct cephalopods had some muscular connection between the hinder part of the body and the shell in the region where the septum joins the shell wall, such a connection would supplement the comparatively feeble attachment of the lateral and annular muscles, and would influence the crumpling of the apex of the visceral cone; or, if there was such a connection directly between the body and the septum, any increase in the area of the latter by folding would increase the effectiveness of such a union; or, not to go beyond the well ascertained facts of observation, such a folding of the septum around its periphery —whether of a goniatitic or ammonitic character—into which the periphery of the hinder mantle penetrated, would enormously strengthen the bond between the animal and its shell, even though they merely remained in juxtaposition and were not directly united.

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THE LIFE CYCLE AND MATING HABITS OF THE MALE TARANTULA

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THE tarantula, *Eurypelma californica* ausserer, is very common in a number of our southwestern states, such as California, Arizona, New Mexico, Texas, Oklahoma, Arkansas, and probably others. In Arkansas it occurs in smaller or greater colonies in various regions where conditions with reference to shelter and food are favorable. Hillsides in meadows, or woodland not completely shaded, that are relatively free from weeds and tall grass, may be regarded as suitable ground, especially if numerous flat rocks of medium size are available for shelter. Although the spiders can and do dig their holes, they very frequently do no more than dig an entrance underneath a large flat rock, where they may live for several years.

A colony of from twelve to fifteen spiders is located near the university campus, and has been under fairly close observation for nearly nine years. For more intensive study, a varying number of tarantulas have been kept in the laboratory where they are placed singly in large battery jars, provided with an inch or two of soil and a dish with water. The jars are covered with screen wire tops. If the spiders are kept in a cold room, they will not require any food from early in October till late in March. During the rest of the year, they are fed on live grasshoppers, cockroaches, caterpillars, and some other insects. A full grown tarantula will require no more than one large grasshopper, such as *Melanoplus differentialis*, every five or six days. The small tarantulas, up to two-and-a-half years old, are fed on termites.

The sexes in mature tarantulas are readily distinguished by the fact that the males have longer legs in comparison with the size of the body, and by the relatively short and somewhat club-shaped palpi.

In the field observations the males have till recently been very puzzling. In spite of much diligent searching in many places, I have never seen a male out of doors except during the mating season. (In the Canal Zone, I have seen the males at night sitting presumably in front of their own holes, just as the females were doing. This was in August. Whether it was the mating season, I cannot say.) At this time the males may be seen sitting near the holes occupied by females, or wandering about in the neighborhood of these holes. The mating season extends through most of the months of September and October. All the males that have been brought into the laboratory died soon after the mating season was over, usually during the month of November. One male lived through the winter and till the following July.

This account of the life cycle is based

on observations made on a number of spiders in various stages of development, have been under observation throughout their life time from hatching till death

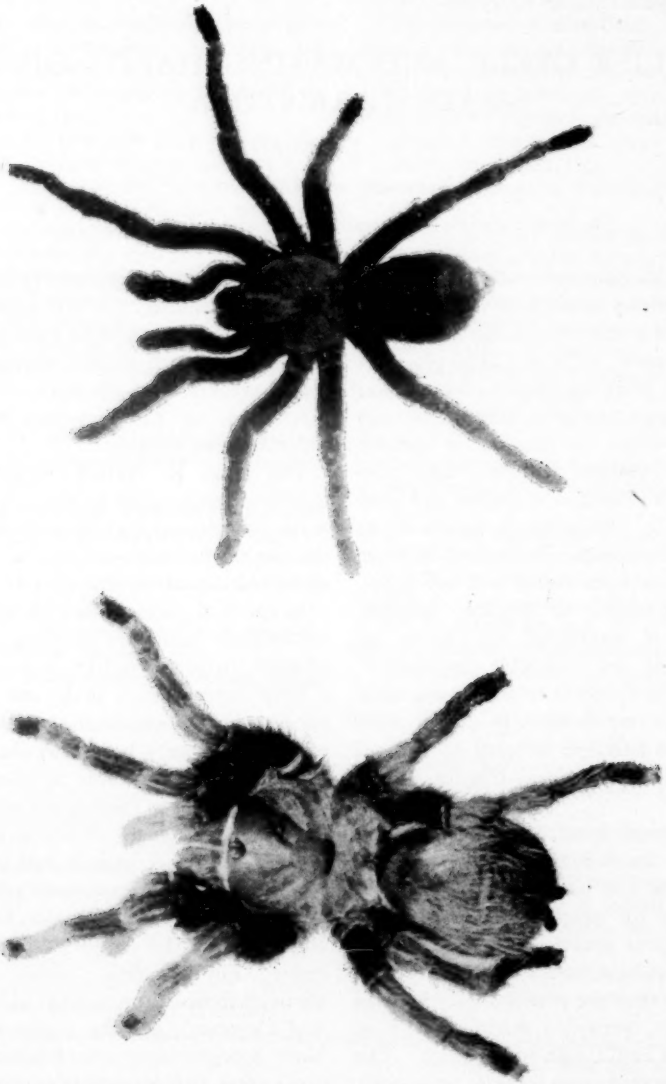

FIG. 1. ABOVE: MATURE MALE TARANTULA. BELOW: FEMALE TARANTULA 14 TO 16 YEARS OLD
(Photograph by David G. Hall)

ranging from newly hatched individuals to fully matured adults. No individuals after maturity; but the observations that have been made for a number of years on

spiders of various sizes will probably serve to make out a reliable account of the entire life cycle.

GROWTH

Measuring the total length of the spider at certain intervals of time is obviously not a very exact way of observing the growth; for the abdomen may vary in size between fairly wide limits. The increase in the length of the carapace is perhaps a more reliable indication of the growth; but since the records of this have been kept for only a few years, they are not suitable for use here.

The rate of growth of tarantulas from the time of hatching until the age of three-and-a-half years has been observed (see accompanying table), as has that of somewhat older tarantulas of various sizes. By putting these figures together, a table has been constructed which represents with a fair degree of accuracy the annual growth throughout the entire life cycle of a male tarantula.

Regarding the estimate of the ages of the various spiders represented in the table, some explanation is perhaps desirable. Although WF, when first measured, was 18 mm. long and but slightly longer than McI_6 at the age of three-and-a-half years, the former has been estimated at a year older, for the reason that conditions in the laboratory are more favorable than those out of doors. The unusual growth that it made during its first year and a half in the laboratory lends support to this assumption. At the age of eight-and-a-half years it measured 37.4 mm. RT_1 when first measured was 37.5 mm., and therefore fitted well into the age of eight-and-a-half years. This male reached maturity last fall (1927) at an estimated age of eleven years. There is a possibility that his age was one year less than that, but it is more likely that he was older, perhaps twelve years.

The tarantulas probably do practically all their hunting right in front of their holes, where they patiently wait night after night for a suitable beetle, cricket, or other insect. They locate their prey wholly by the sense of touch. Thus a cricket may come within a centimeter of where the tarantula is waiting, and be perfectly safe; however, as soon as one touches the other, the cricket is very speedily brought in reach of the fangs and consumed. From this method of hunting, it seems obvious that the tarantulas must often undergo longer or shorter periods of fasting. And from observations in the laboratory, it appears that Nature has equipped them well for this; for they can easily go without food for a month or six weeks and probably longer. As a result of the fasting, the time required

ANNUAL INCREASE IN SIZE

(In millimeters)

	½ YEAR	1½ YEARS	2½ YEARS	3½ YEARS	4½ YEARS	6 YEARS	6½ YEARS	7½ YEARS	8½ YEARS	9½ YEARS	10½ YEARS	11½ YEARS
WH_2	6.8	10.8	16.6									
McI_6		10.0	13.3	17.6								
WF					18.0	28.0	32.5	35.2	37.4			
RT_1									37.5	46.4	48.5	47.3

Measurements were made during the winter, from the last week in December till the first week in February, except the 6-year record, which was taken in the following July.

for reaching maturity will probably vary by as much as two years.

If the observations made on the several spiders may further be applied to RT_1, the mature male, he has gone through the following molts: the first molt about three or four weeks after hatching, when emerging from the cocoon; four molts in the following year; two molts in each of the next seven years; and one in each of the last three years, making a total of twenty-two molts for the entire life cycle.

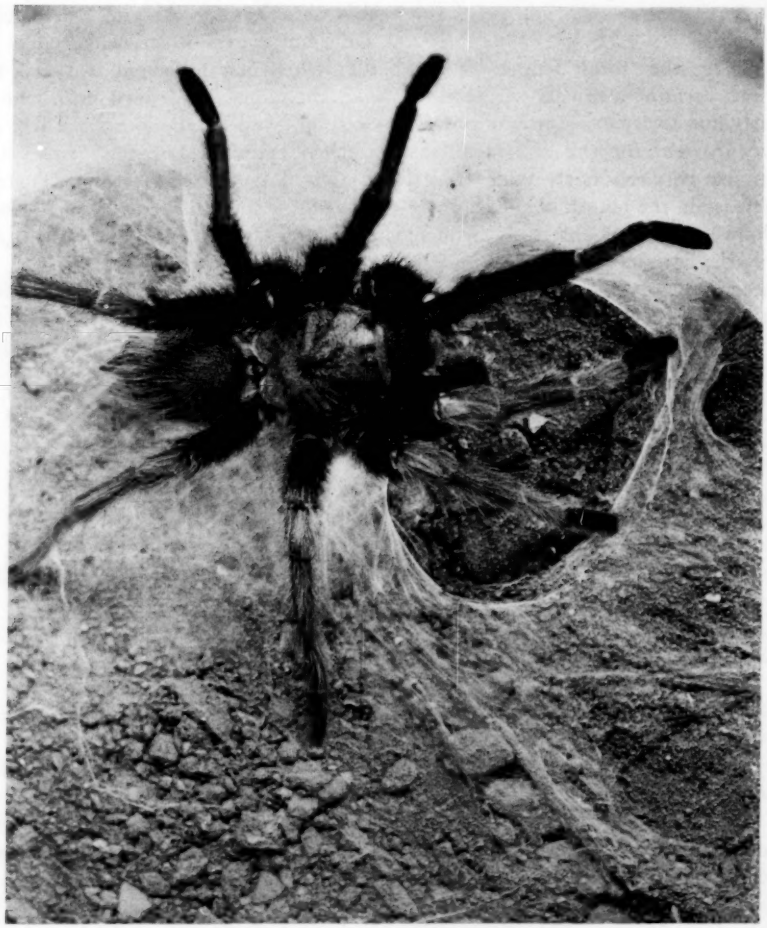

FIG. 2. MALE TARANTULA OVER SPERM WEB
(Photograph by W. J. Baerg)

During the four years that RT_1 has been under observation, he was taken for a female. The legs apparently resembled

in proportion to the body, those of the female, and the palpi were relatively long and slender like those of a female. When he went through the last molt he emerged from the old skin, a mature and fully equipped male. The suddenness with which he changed from the state of adolescence to ripe manhood is striking. His transformation, coupled with the fact, already mentioned, that all the males brought into the laboratory died soon after the mating season, explains why adult males are never seen out of doors except at mating time.

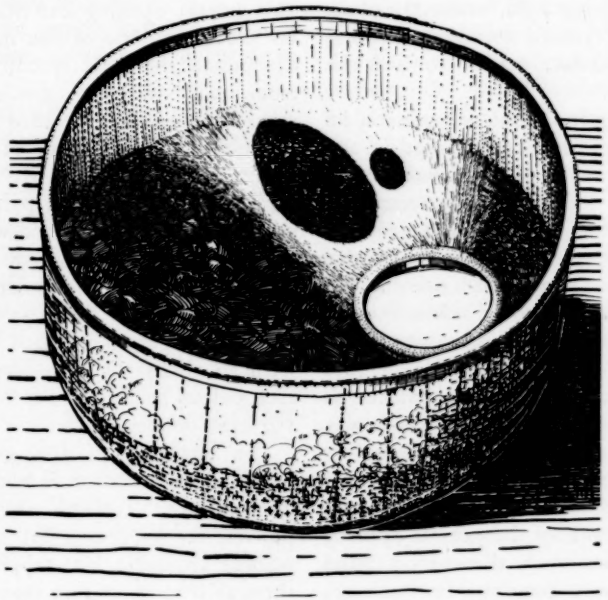

FIG. 3. SPERM WEB IN BATTERY JAR
(Drawing by David G. Hall)

MAKING THE SPERM WEB

After attaining maturity the male is not slow to realize Nature's purpose in his life. On the sixth day after the last molt (August 28), he made his first sperm web and presumably charged his palpal organs. Ten days later (September 7), a second web was made; five days later a third (September 12); and eighteen days later (September 30), a fourth. This last web was made twenty-four hours after he had mated with one of the females in the laboratory. The making of this fourth web, his last one, I was able to observe.

The web was made in a battery jar nine inches in diameter. On one side the web was fastened to the soil at the bottom, and on the other side on the wall of the jar. The male began weaving at 9:20 a.m. As his abdomen swung right and left, the spinnerets moved gracefully up and down, touching here and there to fasten the threads. With the hind legs, he felt for the proper place of attachment of

threads, determined where the web needed to be strengthened, and outlined in a general way the two openings. This weaving was done while the male stood over the web, and was finished in forty minutes. The male now turned around several times while examining and reinforcing the web, and then facing towards the large opening and putting the first two pair of legs forward, he moved forward and turning over on his back slid easily through the large hole, under the web. Thereupon he turned around, remaining on his back but facing again towards the large opening.

After resting for about one minute, he proceeded with the second stage in the construction. This is done while the male is on his back, and is mainly the strengthening of the margin around the small oval opening, and in particular the narrow band between this opening and the large one. This band when finished is quite thick, and densely woven, much more so than the rest of the web. This stage of the construction was finished in fifteen minutes, and the web was completed.

Then the male brought the ventral surface of the abdomen up against the web, so that the margin of the genital opening was in contact with the narrow band between the two openings in the web. By moving the abdomen from side to side and pressing against the band, he rubbed the margin of the genital opening for a period of twenty minutes. During this time he was also stroking the genital bulbs. The fangs were partly opened and the bulbs were drawn through between the fang and the row of teeth. This process seemed very thorough and elaborate. The hair near the fangs appeared rather shiny, but careful examination through a binocular lupe failed to show any moisture. From time to time in this stroking process the fangs would open wider than usual and gently clasp the distal portion or tarsus of the palpus.

The process of rubbing the margin of the genital opening (doubtless for the purpose of stimulating the sex glands) and stroking of the genital bulbs continued for fifteen to twenty minutes. Then the droplet of spermatic fluid appeared in the genital opening and was deposited on the under side of the narrow band. Thereupon the male speedily came out from under the web, got on his feet, turned around and proceeded at once with the tapping or charging of the genital bulbs. Sitting over the web so that his cephalothorax projected partly over the smaller opening, he tapped with the tips of the bulbs alternately in the drop of spermatic fluid on the under side of the narrow band. At first the tapping was slightly irregular, but soon it proceeded with an almost machine-like regularity, each palpus beating at the rate of 135 to 150 taps a minute.

The charging of the genital bulbs occupied the male for an hour and forty-five minutes. Towards the end of the process, he tapped a bit slower, then walked around a bit, tapping here and there as if to make sure that all the fluid had been taken up. Then he seized the web with both fangs, pulled backward, and stooping down to get a better hold on the web, he walked forward and took practically all of it with him. After tapping the ground a few times with his palpi he settled down to rest. Later in the afternoon, I placed a female in the jar with the male, but he was not in the mood for mating. On the afternoon of the following day, this was tried again and mating took place.

MATING

The mating process of *Dugesiella hentzi* has been very fully described by Dr. Alexander Petrunkevitch of Yale. Dr. Vital Brazil gives a brief description of the mating of *Gramnostola longimana* and *G. acteon*. Among the higher spiders, the mating of the house spider has been carefully observed and described by Dr. H. E. Ewing of the U. S. National Museum. Wilhelm Bölsche gives a vivid account of the mating habits of *Araneus diadematus* (*Epeira diademata*), a European species.

It is relatively easy to observe the mating of tarantulas. If a male is brought in during the mating season and put with a female, mating is likely to take place provided the male has provided the bulbs with spermatic fluid. If not, he may be kept a few days until this has been done. The females will mate several times, as Dr. Petrunkevitch has observed in *D. hentzi*. One female mated thirteen times with four different males.

Mating in *Eurypelma californica* has been observed ten or twelve times. The male to whom this account is largely devoted mated twice with the same female. My notes of his first mating will perhaps serve to describe what usually takes place:

> When the male was placed in the jar with the female she at once put on a belligerent attitude, rising on her hind legs and spreading her fangs. The male advanced very boldly and rising up likewise, he soon had her fangs caught on the spurs of his front legs. He did not raise her up much, but bent her upper half decidedly backwards so that her body was bent almost at a right angle. After a good deal of fumbling and tapping on the sternum of the female, the male introduced first the bulb of the left and later that of the right palpus. After withdrawing the latter, he waited for about one-half minute, and then very deliberately he withdrew from the female. Mating occupied about one minute's time. The female made no attempt to attack the male after the mating act.

When this male mated the second time, twenty-four hours after the making of the sperm web, he introduced both palpi twice. This has been observed in several instances.

When putting a male and a female together in an attempt to observe mating, it is well to make one of them move until it touches the other. This not only apprises them of each other's presence, but also reveals at once the inclination or disinclination for mating. If mating is to take place, they will proceed at once; if not, no amount of coaxing will induce them to do so. Frequently when the male has just touched the female with one of his front legs, and she does not show any visible response, he will slap her vigorously several times, which brings prompt action. She at once rises, spreads her fangs, and the male proceeds. When the male has just secured the fangs of the female in his spurs, she usually stands quite erect. At the introduction of the bulb of the first palpus she relaxes so that the abdomen may touch the ground.

In the majority of the matings that have been observed the female made no serious effort to attack the male at the close of the act. However, the male is almost always very careful in his departure. He moves away as far as possible before he releases her fangs and then he retreats very hastily.

The males of *Dugesiella hentzii* that Dr. Petrunkevitch observed all died toward the end of the month of November. The same has been observed in most of the males of *Eurypelma californica*. One of the males taken in the fall of 1923 lived till the 26th of the following July. This year (1927) one of the males brought in from the field lived till December 27. The male RT_1 is still living, and judging by his present condition, he will live through the winter. It may perhaps be

assumed that the unusual prolongation of the life of this male is due to the regular and abundant food supply furnished during the last four years of his life.

Soon after the mating season the males begin gradually to fail. The abdomen begins to shrink slowly, and the spider gets more and more sluggish. Finally the abdomen is nothing more than a shrivelled and deeply wrinkled prolongation of the cephalothorax, yet the male with the legs drawn up close to the body will live on for several days or even a week. It seems an excellent picture of death due to old age, a gradual and complete exhaustion of all the sources of energy.

The females present a very different picture. At the age of eleven they are probably not even mature. Records, as yet not quite complete, show that the females become sexually mature when twelve or thirteen years of age. One female that was brought into the laboratory when fully matured, fourteen to sixteen years old, is now, nine years later, still in a very healthy and vigorous condition.

SUMMARY

The tarantula, *Eurypelma californica*, common in a number of the southwestern states, has been under observation for about nine years, with the result that the life cycle and the mating habits of the male are fairly definitely known. The life cycle from hatching till sexual maturity is about eleven years, with the possible variation of one year more or one year less. During this time, a male undergoes about twenty-two molts. Until the last molt the male is indistinguishable from the female.

As many as four sperm webs are made by one male, indicating that he will mate at least four times. In the preparation for mating the stimulation of the sex glands is so thorough and deliberate that it seems strange for so low a form of animal life. Mating has been observed ten to twelve times.

After the mating season the males soon decline in vigor. Shrinking and becoming more and more sluggish for some time, they die apparently as a result of a total exhaustion of all sources of energy.

The females, judging by records not quite complete, become mature when twelve or thirteen years old. After attaining maturity, they will live for a number of years; it is not known how many, but certainly till they are twenty years old and probably much older.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

HUMAN SAPIENCE

Being a review of *The Abilities of Man: their Nature and Measurement*. By C. Spearman, Ph.D., F.R.S. New York (Macmillan), 1927. $5\frac{3}{4}$ x $8\frac{5}{8}$; x + 415 + xxxiii. $4.50.

By Charles P. Winsor, Institute for Biological Research, The Johns Hopkins University

In this book Professor Spearman sets forth his theory of the nature of mental abilities and their variation. This theory was originally put forward by him in 1904, and has been the subject of much debate and controversy ever since. The present work is an exposition of the doctrine and of its present status, intended, one gathers, primarily for the general reader, although there is an appendix giving the principal mathematical demonstrations involved. There is no bibliography.

Professor Spearman begins with a survey of the different theories of mental ability heretofore popular. The most important of these is probably that which "assumes mental ability to lie under the sovereign rule of one great power named 'intelligence.'" Unquestionably, in ordinary life we classify people as clever, stupid, or otherwise, exactly as we call them tall or short. But where we can refine our judgments of height by measuring stature in inches or centimeters, such refinement in the matter of intelligence is less simple. However, mental tests were devised and applied and the results were considered as measuring intelligence. These tests, in one form or another, have been and are being used for all sorts of purposes, and some of their more enthusiastic advocates consider that their possibilities are almost unlimited. For instance, I quote the following from Goddard (Goddard, *Human Efficiency and Levels of Intelligence*. 1920, p. 127): "The intelligent group must do the planning and organizing for the mass, that our whole attitude toward lower grades of intelligence must be philanthropic. . . . Democracy is not impossible even in a group with a large mass of people of relatively low mentality, provided that there is a sufficiently large group of people of high intelligence to control the situation." Such quotations could be multiplied indefinitely; the feeling has been general that we might shortly expect a set of tests which would place everyone in his

proper pigeon hole, to the greater happiness and prosperity of the race.

Unfortunately, there are serious objections to the whole test procedure. As yet, we have no agreement on a definition of what intelligence is. Which mental activities involve it, and which do not? For example, shall we include memory? We find no general agreement. Some testers include it, others exclude it. We even find such authorities as Terman and Thorndike including it at one time and omitting it at others. Again, what about imagination? Or language? Or the power of attention? Or even motor ability? All these are included or omitted, depending on the individual tester. Even sensory perception has advocates on both sides. There is, in short, no agreement as to what constitutes intelligence, or in what mental operations it is to be looked for.

We even find the plea advanced by Terman that it is unreasonable to expect us to define intelligence; that we can measure it without knowing anything about its ultimate nature, just as a physicist can measure an electric current by means of a galvanometer without knowing what the ultimate nature of electricity is. But, as Spearman points out, the physicist knows where to look for his current; he knows that he must read the galvanometer which is in circuit with his current. If he did not know which of his galvanometers was really in the circuit, and had no means of finding out, he could determine very little about his current. In the same way, if we do not know which tests involve intelligence, we can hardly expect to measure it.

Naturally, attempts have been made to remedy this ambiguity. Definitions have been proposed, but without great success. Spencer's definition has often been used—intelligence is that mental power which produces "conscious adaptation to new situations." But we have here introduced two more terms—"adaptation" and "situation"—which, as Spearman shows, are themselves interpreted according to the fancy of the individual psychologist. But even without this, the definition does not tell us what kind of operation produces adaptation, and we are as much at sea as before. Other definitions, to which the same objections apply, are the following: "The power of good responses from the point of view of truth;" "the ability to act effectively under given conditions;" "that which can be judged by the degree of incompleteness of the alternatives in the trial and error life of the individual;" "a biological mechanism by which the effects of a complexity of stimuli are brought together and given a somewhat unified effect in behaviour." One feels that Professor Spearman is right when he advocates abandoning the term "intelligence" as having lost any definiteness it may once have possessed.

But in addition to all this, and supposing that we have defined our "intelligence" satisfactorily, still we have the task of establishing the unity of function of intelligence. But this is just what is probably not true, if we are to accept the results of the tests; for these tests are reported to measure many different functions, so that a high total score tells us nothing about which functions are working well. And worse, each investigator has his own set of functions into which "intelligence" may be analyzed.

The forced abandonment of the unitary "intelligence" leads naturally to the theory that there are broad mental powers, such as "judgment," "memory," "invention," "attention," each of which functions as a unit. Here, again, we have a doctrine which is widely held in the popular mind. In fact, in practice most of us

hold both the previous doctrine of "intelligence," and the contradictory doctrine of "faculties." We talk glibly of our friends' "judgment," "concentration," "imagination," or what not, just as we speak of their intelligence. As soon as we attempt to make the conception of faculties more definite, however, we find ourselves involved in difficulties. There is no general agreement as to what faculties should go on our list; no two psychologists would agree; and as soon as we have invented a list, some other worker can show that some of the faculties which we have considered as functional units ought really to be analyzed further.

The logical conclusion to which this process of analysis leads us is that there exist innumerable elementary abilities, which may be either independent or intercorrelated. Those who adopt this view attempt to justify their mental testing procedure on the ground that they thus secure an average sample of a person's abilities. Spearman points out here that for our average to have any meaning it must be based on a really representative selection, in which all abilities are represented, and in which duplication is avoided. This, however, is just what the present tests do not do. There is not really representative selection. There cannot be, for there is no agreement as to the elementary abilities which are to be tested. Further, there is the question as to whether such a sample would really have any great meaning if we obtained it.

That there is some meaning in the current mental testing is, however, obvious. The curious fact is that tests based on widely different theories, and apparently of widely different forms, do show substantial correlations with each other. Some theory is required to unify the facts. Having disposed, to his own satisfaction, of all the rival theories, Spearman advances his own.

Stated in its simplest terms, the theory is that the achievement of any individual x in any ability a is a linear function of two factors g and s, g being common to most if not all abilities, and s being specific to each ability. Put otherwise, the observed correlation between activities is usually due to the g, which is common to all of them, and only rarely to the fact that they share an s. Or, mathematically, we may write

$$\left.\begin{aligned} m_{ax} &= r_{ag}\, g_x + r_{as_a}\, s_{ax} \\ m_{bx} &= r_{bg}\, g_x + r_{bs_b}\, s_{bx} \\ &\cdots\cdots\cdots\cdots \end{aligned}\right\} \text{for any individual } x \quad (1)$$

$$\left.\begin{aligned} m_{ay} &= r_{ag}\, g_y + r_{as_a}\, s_{ay} \\ &\cdots\cdots\cdots\cdots \end{aligned}\right\} \text{for any individual } y$$

Such a system we shall refer to as a (g, s) system.

Now if we accept this theory, certain results can be derived from such a set of equations. We assume that the correlations of g with any s, and of one s with another, are all zero. Then the correlation of one ability with another will be due entirely to g, and we can show, with a little algebra, that

$$r_{ab} = \frac{r_{ag}\, r_{bg}\, \sigma_g^2}{\sigma_a\, \sigma_b},\ r_{ac} = \frac{r_{ag}\, r_{cg}\, \sigma_g^2}{\sigma_a\, \sigma_c},\ \text{etc.},$$

and that

$$r_{ab}\, r_{cd} - r_{ac}\, r_{bd} = 0 \quad (2)$$

The quantity on the left of equation (2) is termed by Spearman the "tetrad difference" of the correlations involved. We shall write (ab, cd) for this quantity. It is, of course, evident that four abilities will (by permutation of the subscripts) give us six tetrad differences, three of which will be numerically equal but of opposite sign to the other three.

The importance of the tetrad difference in Spearman's theory is that he makes it the criterion by which the whole theory is to be judged. It has been shown that if

$(ab, cd) = 0$ for all tetrads obtained from a table of correlations, then the abilities involved can be analyzed into a (g, s) system, and that if $(ab, cd) \neq 0$, no (g, s) system can be found; we shall require some more complicated system. Spearman's procedure in any given case, then, is to construct a table showing the intercorrelations of abilities, as measured by tests or otherwise, and to determine whether or not the tetrad difference vanishes. If it does, the abilities involved can be analyzed into the form of equations (1).

In practice, of course, the correlations which we obtain will always be affected by sampling errors, and accordingly our tetrad differences will not in general be zero even if they are derived from a (g, s) system, but will tend to fluctuate around zero. It therefore becomes important to determine the permissible range of fluctuation within which we may regard the tetrad difference as sensibly zero. This requires, clearly, determining the theoretical standard deviation of a tetrad difference in terms of the correlations on which it is based. This can be done by the usual procedure; and Spearman proceeds to make comparisons of the observed values of his tetrad differences with the theoretical probable error (derived by the usual convention that the p.e. $= 0.6745\ \sigma$). Now this assumes, among other things, that the frequency distribution of tetrad differences is approximately normal. This, however (as was pointed out in a review in *Nature*, August 6, 1927, pp. 181–183) is by no means even a plausible assumption. We know that, for small samples and for even moderately large correlations, the frequency distribution of correlation coefficients is widely different from the normal. Further, in a table of tetrad differences, the individual differences have correlation (over and above that due to their limited number) due to the fact that the same correlation coefficient enters into different tetrads. Thus the presence of a common element will introduce correlation between such quantities as (ab, cd) and (ae, fg). What kind of frequency distribution might result is by no means obvious; but to assume it Gaussian seems clearly unjustified until we have at least experimental evidence that it is approximately so. We should feel easier in our minds if Professor Spearman had given a frequency distribution of tetrad differences for a set of correlations actually known to be derived from a (g, s) system.

Professor Spearman does, however, give us something upon which to form an idea of how tetrad differences may vary. He has taken two tables of correlations of mental tests, in one of which 14 tests were applied to 37 persons, and has worked out the frequency distribution of tetrad differences for the two cases. Upon the frequency distributions so obtained he places normal curves having standard deviations equal to the theoretical and mean standard deviations of the tetrad differences of his tables. Graphically, the fit is good; but unfortunately he gives only a graphic comparison. The reviewer in *Nature*, cited above, stated that an actual goodness of fit test indicated that the fit is really very bad in one case, and distinctly not good in the other.

Hoping to obtain more light, I have myself calculated for the correlations of W. Brown, cited by Spearman (p. 147) the frequency distribution of tetrad differences. In this case I find that a normal curve will not give even an approximate fit; and that even the Pearson Type VII curve indicated by the values of the observed moments is an extremely bad fit to the data. On the other hand, the difficulty in the fit is that the tetrad differences are more closely concentrated about

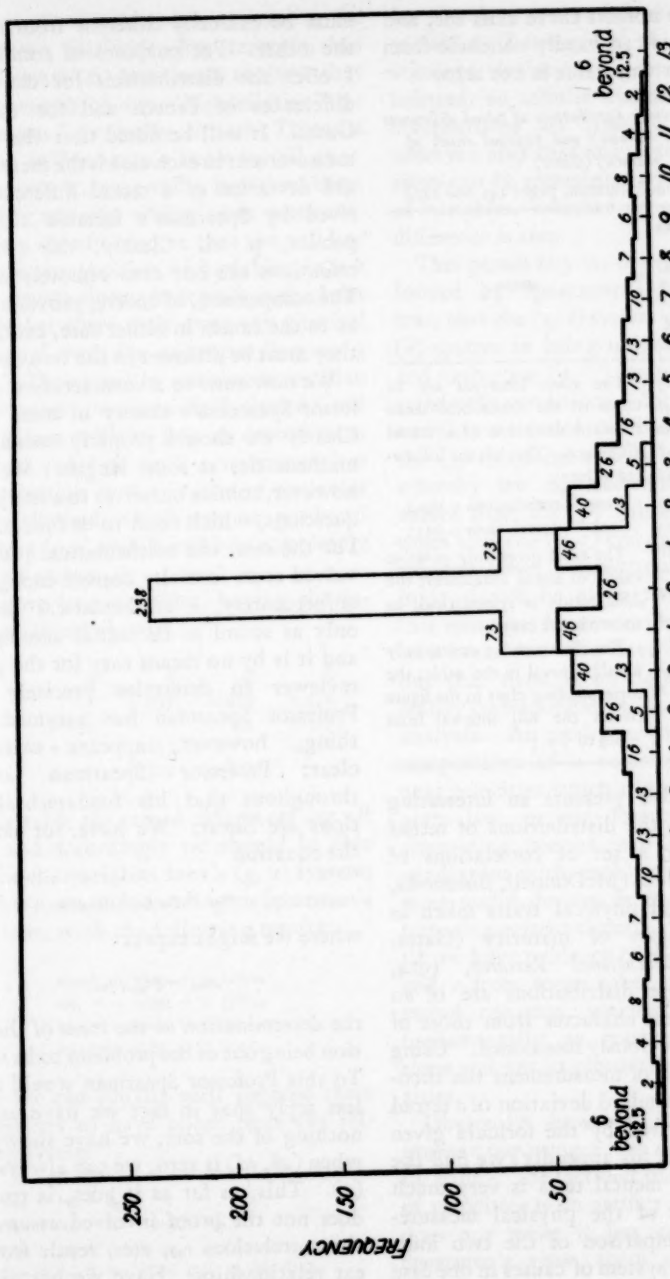

FREQUENCY
250
200
150
100
50
6 beyond -12.5
-13 -12 -11 -10 -9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12 13
6 beyond 12.5
TETRAD DIFFERENCES IN MULTIPLES OF THEORETICAL MEAN STANDARD DEVIATION

FIG. 1. COMPARISON OF FREQUENCY DISTRIBUTIONS OF TETRAD DIFFERENCES FOR MENTAL TESTS (BROWN) AND FOR PHYSICAL TRAITS OF MATURITY (GATES).

zero than the normal curve calls for; and accordingly we can hardly conclude from this that their true value is not zero.

Comparison of frequency distributions of tetrad differences for mental tests (Brown) and physical traits of maturity (Gates)

(Calculated from Spearman, pages 143 and 147)

CLASS INTERVALS	NUMBER OF TETRAD DIFFERENCES		NOTES
	Brown	Gates	
0 – 0.5	119	13	The class intervals are in terms of the theoretical mean standard deviation of a tetrad difference. This has the following values:
0.5– 1.5	73	46	
1.5– 2.5	13	40	
2.5– 3.5	5	26	
3.5– 4.5		16	Brown's correlations 0.0524
4.5– 5.5		13	Gates' correlations 0.0333
5.5– 6.5		13	
6.5– 7.5		10	The table gives only positive values of tetrad differences; the distribution is symmetrical, as shown in the curve.
7.5– 8.5		7	
8.5– 9.5		6	
9.5–10.5		8	
10.5–11.5		4	The class 0 to 0.5 covers only a half interval in the table; the corresponding class in the figure covers the full interval from −0.5 to +0.5
11.5–12.5		2	
over 12.5		6	

Spearman also presents an interesting comparison in the distributions of tetrad differences for a set of correlations of bodily dimensions (McDonnell, *Biometrika*, 1901, 1) and of physical traits taken as indicating degree of maturity (Gates, *Journal of Educational Research*, 1924, p. 341). These distributions are of an entirely different character from those of mental tests previously mentioned. Using as our standard of measurement the theoretical mean standard deviation of a tetrad difference (derived by the formula given by Spearman in his appendix) we find the scatter of the mental tests is very much less than that of the physical measurements. A comparison of the two indicates that the system of causes in one case must be radically different from that in the other. For purposes of comparison, I offer the distributions for the tetrad differences of Brown and for those of Gates. It will be noted that the unit of measurement in each case is the mean standard deviation of a tetrad difference, derived by Spearman's formula 16A, Appendix, p. xi. Clearly, the two distributions are not even remotely similar. The comparison, of course, proves nothing as to the causes in either case, except that they must be different in the two cases.

We now turn to a consideration of Professor Spearman's theory in more detail. Clearly we should properly consider his mathematics at some length. We shall, however, confine ourselves to a few general questions, which seem to us fundamental. For the rest, the mathematical proofs involved seem formally correct enough; but unfortunately, a mathematical proof is only as sound as its initial assumptions, and it is by no means easy for the present reviewer to determine precisely what Professor Spearman has assumed. One thing, however, appears reasonably clear; Professor Spearman assumes throughout that his fundamental relations are linear. We have, for example, the equation

$$m_{ax} = r_{ag}\, g_x + r_{as_a}\, s_{ax}$$

where we might expect

$$m_{ax} = f(g_x, s_{ax})$$

the determination of the form of the function being one of the problems to be solved. To this Professor Spearman would doubtless reply that in fact we have assumed nothing of the sort; we have shown that when (ab, cd) is zero, we can always write (1). This, as far as it goes, is true; but does not the proof involved assume that the correlations r_{ab}, etc., result from linear relationships? Have we not assumed

linear regressions throughout, and is the assumption justified? For example, has any adequate test been made to show that the regression of, say, "Cancellation" on "Opposites" is really linear? There is nothing in Spearman's book to tell us.

To return to our g and s, however, there are other remarks which seem pertinent. First, we should observe that the validity of the decomposition of variables into a (g, s) system does not depend in the least on whether there truly exist any physical or mental realities corresponding to g and s. They need be nothing more than a convenient mathematical fiction; and their values will be just as determinate. The best proof of such a statement is a demonstration that a system of variables can be devised which can be produced both by a (g, s) system and by a completely different system.

Suppose four variables, having the intercorrelations shown:

	A	*B*	*C*	*D*
A		0.895	0.694	0.578
B	0.895		0.633	0.517
C	0.694	0.633		0.408
D	0.578	0.517	0.408	

In this table the tetrad differences are all zero, and accordingly we should be able to split the variables into a (g, s) system; which we can do, according to Spearman's equations, with the following results:

$$m_{ax} = 0.994g_x + 0.106s_{ax}$$
$$m_{bx} = 0.899g_x + 0.438s_{bx}$$
$$m_{cx} = 0.702g_x + 0.712s_{cx}$$
$$m_{dx} = 0.578g_x + 0.814s_{dx}$$

But we can equally well suppose these correlations to have arisen from the following system

$$m_{ax} = v_{1x} + v_{2x}$$
$$m_{bx} = v_{1x} + v_{3x} + v_{4x}$$
$$m_{cx} = v_{1x} + v_{2x} + v_{3x} + v_{5x}$$
$$m_{dx} = v_{1x} + v_{2x} + v_{3x} + v_{6x} + v_{6x}$$

in which v_1, v_2, etc., are independent variables (having, in this case, equal standard deviations). And, as may be inferred, an infinite number of other decompositions are possible. It is to be observed also that any system of correlations can be represented by such a system of variables, whether or not the tetrad difference is zero.

This possibility is, of course, not overlooked by Spearman. He points out, first, that the (g, s) system differs from our (v) system in being unique; there is one and only one (g, s) system which will satisfy the conditions. Second, he points out that a relation can be set up between the (g, s) system and such a (v) system, whereby we can determine the (g, s) values from the (v) values. Finally, he urges that the (g, s) system is simpler and requires fewer assumptions, and accordingly should be given preference. With this question, however, we need not concern ourselves. We have merely pointed out that there is no necessary physical reality corresponding to the mathematical analysis. An analogy would be the decomposition of a velocity into component velocities which add by the parallelogram law, or the decomposition of an alternating current into components in quadrature with each other—one of the most useful devices in the theory of alternating current circuits. Unless and until we have evidence of the existence of g and s from some other source than the tetrad equation, we must regard them fundamentally as mathematical expressions and not as physically existing quantities.

Obviously, however, this should not prevent our using g and s if they are useful to us. The fact that the decomposition of velocities is an artifice of mathematics does not make it less useful. And, in Spearman's view, there are grounds for

believing in the physical existence of g and s.

Another point which seems important is the following. Professor Spearman writes $m_{ax} = r_{ag}\, g_x + r_{as_a}\, s_{ax}$, in which r_{ag} and r_{as_a} are constant for all individuals. Now, even if we allow that the relation connecting m_a with g and s is linear for any individual, it seems to involve an additional, and a rather considerable, assumption to say that the relation shall be the same for all individuals tested. Assuming that g and s really correspond to physical quantities, is there *a priori* any reason for assuming that they must have the same coefficients for all individuals tested? Must we have

$$m_{ax} = r_{ag}\, g_x + r_{as_a}\, s_{ax}$$

and

$$m_{ay} = r_{ag}\, g_y + r_{as_a}\, s_{ay}$$

rather than this relation?

$$m_{ax} = A g_x + B s_{ax}$$
$$m_{ay} = C g_y + D s_{ay}$$

Of course, we return immediately to the proof of the existence of the (g, s) system provided (ab, cd) vanishes throughout. However, it appears that Spearman himself recognizes that r_{ag} and r_{as_a} remain constant only so long as the populations tested are sufficiently homogeneous. We find him saying (p. 217 *et seq.*): "Another important influence upon the saturation of an ability with g appears to be the class of person at issue. The most drastic example of this is supplied by a comparison between normal children and those who are mentally defective. . . . . The correlations are much smaller in the case of the normal children. This indicates that with these the influence of the energy [g] has gone down and that of the engines [s] has correspondingly gone up. . . . . No less marked is the tendency on comparing children with adults. As exemplifying this may be taken the correlations obtained by Otis and Carothers respectively for what appear to have been similar tests in each case:

TESTS	CORRELATIONS WITH g	
	Otis, Grades IV–VIII	Carothers' students
Analogies	0.84	0.71
Completion	0.88	0.53
Directions	0.86	0.45
Digits, memory	0.41	0.22

"Similarly, Stead has found that even motor abilities have considerable correlations with tests of g up to about 11–12 years of age, but not later."

We seem to find, then, that while in deriving our theory we showed that r_{ag} and r_{as_a} should be constant for all individuals, in actual practice they vary from group to group. But if from group to group, why not within the group? In fact, we find Spearman going on from what we have just quoted as follows (p. 219): "Now, all the changes we have been considering follow a general rule. The correlations always become smaller—showing the influence of g on any ability to grow less—in just the classes of persons which, on the whole, possess this g more abundantly." But there seems to be no clear reason for supposing, if this is true for different classes, that it is not true for individuals within the class; and if this be true, it would appear that any theory which involved a linear relation between achievement, g, and s, could not be correct.

Of course, we still need not throw the theory overboard. It may well be that, provided we keep our group sufficiently homogeneous, we can maintain our linear relation; which amounts to saying that

for relatively small changes in *g*, the variation in achievement will be linear. But it would appear that for any complete theory we should require something much more elaborate than the linear (*g*, *s*) system.

So far we have not been concerned at all with what, if anything, *g* and *s* really are; with what physical facts they may be identified. Spearman, after rejecting the various explanations which have been made, suggests that we may regard *g* as a general mental energy, while the various *s*'s may be taken as the various engines in which this energy is utilized. The language, especially as applying to the engines, is somewhat vague; but Spearman nowhere, so far as I have found, explains his conception clearly. The hypothesis as stated seems scarcely likely to attract a physicist; to assume that output is given by the sum of the energy input and the efficiency of the engine is an unusual formula. We might, of course, say that we are dealing with logarithms; but there would appear to be difficulties here. In any case, the hypothesis seems scarcely of vital concern in the present state of the whole theory. If, of course, it were found possible to measure mental energy directly, the case would be different; but until we have some means for measuring it, it seems idle to waste much time identifying it with a factor *g*, whose very existence, even as a matter of mathematics, is still questionable.

There are other difficulties which will occur to any reader. One such lies in the highly variable nature of the measurements obtained, and of the results deduced from them. For example, on pages 202 and 203 Spearman cites the correlations with *g* which have been found by various workers for different tests. The test of "Opposites" appears three times, with correlations with *g* of 0.89, 0.71, and 0.37. Obviously, such values, if obtained in any biometric investigation, would indicate that something was radically wrong. Whether they really indicate that here, it is impossible to say, because we do not know that the three "Opposites" were really the same thing. However, we may reasonably infer from the fact that Spearman refers to them all under the same names, and without indicating in any way that they are different tests, that they are intended to be similar tests and to measure the same thing; and we are forced to conclude, either that the tests themselves were badly devised, or that the quantities correlated cannot be measured in this manner.

This difficulty, of the large variability of the measurements obtained in similar mental tests on the same subject, has of course attracted the attention of psychologists, and Spearman has devised a formula for eliminating its effect. This formula he calls the correction for "attenuation." The proof of it, and the circumstances under which it may legitimately be used, would lead us too far; and according to Spearman, it is unnecessary to use it in order to establish the vanishing of the tetrad difference. A remark of Spearman's about it (Appendix, p. i, note) may, however, be quoted: "It should be noted that the correction for attenuation only has, and only can have, the virtue of producing *on an average* the true amount of correlation. Hence, if this true amount is close on unity, the correction will in nearly half the cases produce values *greater than unity*, although no such amounts of correlation are actually possible." (Spearman's italics.) Without questioning the validity of the correction, one can merely report a certain uneasy visceral sensation when correlation coefficients greater than unity are mentioned.

We have devoted the bulk of this review to a consideration of the basic doctrine, and very little space is left for an exposition of the remainder of the book—which bulks rather larger than the portion we have examined. In the rest of the book Spearman builds his theory into an imposing edifice. This construction, however, rests entirely on the fundamental proposition that the decomposition of abilities into *g* and *s* is really valid. There are, however, some interesting results obtained. In particular, he devotes a good deal of attention to the search for general factors other than *g* common to numerous abilities. He claims to find such a factor (which he calls *w*) in the "consistency of action resulting from volition;" and he finds another factor, called *c*, whose precise nature is not quite clear, but which presents some interesting correlations with various traits of character. A selection of these (quoted from page 355) follows:

Sense of humor	0.98
Pure-mindedness	−0.45
Originality of ideas	0.88
Interest in religion	−0.39
Suggestibility	−0.29
Profoundness of apprehension	0.59

In conclusion, we may say that Professor Spearman seems to us to have fallen a long way short of establishing his theory. On the other hand, he has made out enough of a case to call for the serious consideration and investigation which his book will undoubtedly receive.

[The current issue of Biometrika (Dec. 1927, pp. 246–291) which appeared while this review was going through the press, contains a long analysis and criticism, by Pearson and Moul, of Professor Spearman's mathematics. The conclusion is there reached that the tests provided by Spearman are mathematically entirely inadequate to establish his theory; and in particular, that his formula for the standard deviation of a tetrad difference is in error. Accordingly, some of the statements made above may require qualification; but the conclusions reached still seem sound.]

BRIEF NOTICES

EVOLUTION

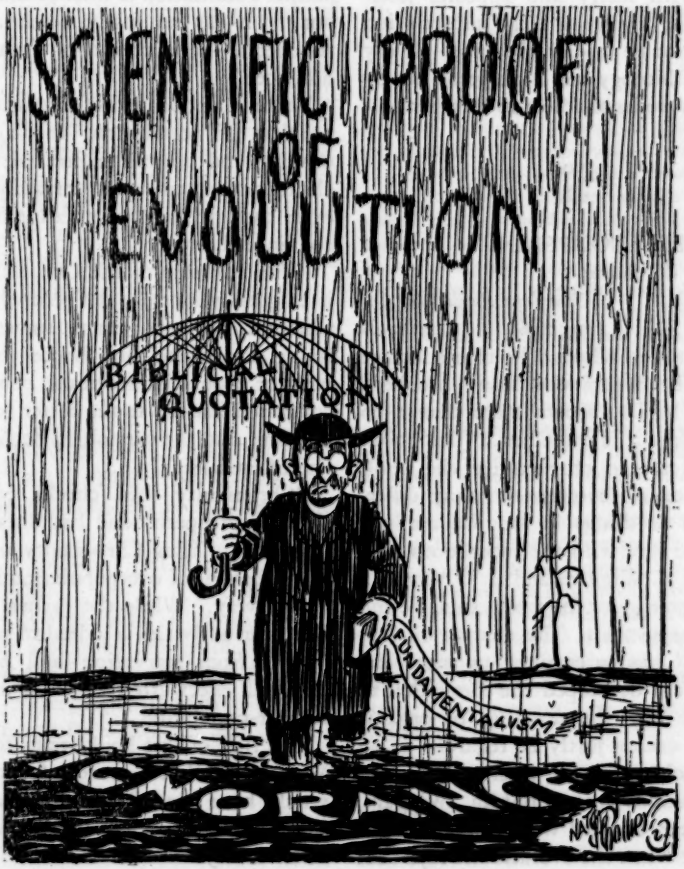
EVOLUTION.

Evolution Publishing Corporation
96 Fifth Ave., New York

Annual subscription $1.00

8 x 11

We are delighted to welcome this new journal, which has as one of its nobler purposes the exploitation of the fun in Fundamentalism. The cartoon which we reproduce here from the first issue is indicative of the earnestness with which this purpose is to be pursued. Reginald, our Office Boy, says he thinks it is too bad that they dressed the parson up in a Church of England uniform, instead of clothing suitable to the Baptist or Methodist he really is. We are disposed to agree with Reginald. The reverend clergy are by no means all Fundamentalists, and when one is embarking upon an organized



campaign of mayhem it is just as well to be discriminatory. If all the biblical brothers were as intelligent as, on the average, are those who perform the Episcopalian mysteries perhaps there would be no necessity for the evolutionary cohorts to gird their loins.

"Evolution" is going to be an entertaining little paper, if one may judge by the first number. David Starr Jordan, William K. Gregory, and Henshaw Ward contribute significant and readable articles and the editorial staff dresses up the number with merry and apposite jests. At a dollar a year a large subscription list ought to be readily obtained. Every teacher of biology can have great fun by giving his students access to this periodical.

THE SUPERFLUOUS MAN.
By Milton W. Brown.

Standard Publishing Co.
$2.00 5⅛ x 7½; 296 *Cincinnati*

It is stated in Who's Who that a lecture called "The Superfluous Man" has been delivered by Dr. Brown more than 1500 times. Now it is embodied in this book. It is difficult to characterize the book briefly because there are so many different kinds of things in it. We are not even quite sure who the superfluous man is, but A. E. Wiggam and E. G. Conklin seem to come in for the most extensive and severe disapproval. The chapter on "Intolerance" has entertained us most, because in it is developed the thesis that to forbid by law the teaching of organic evolution cannot justly be regarded as an act of intolerance. By a series of ingenious quotations from Conklin, Wiggam, and Coulter, coupled with the neat argument that when the evolutionist says that fiat creation is unthinkable he overlooks the fact that every artist does this very thing as a part of his job and that what such mere men can do will certainly be no difficulty at all for God, the reader is led to the following conclusion: "In view of the foregoing statement by a great scientist [Coulter], it becomes perfectly clear to the layman that the insistence, the great outcry about liberty of thinking, relative to the Tennessee law forbidding the definite teaching, as an established truth, that man descended from a lower order, is neither a limitation of intellectual freedom nor is it—as so many editorials have thundered—an outburst of fanatical ignorance."

There is a good deal of discussion of the problem of population, and again the novelty and unexpectedness of the conclusions reached must certainly amuse, even though they may fail entirely to convince the reader.

"The influence of the Christian church is to greatly increase the prosperity of its members, to impel them toward better living conditions, and hence the movement of population from the country and congested districts to the better residential districts, and the very sharp decline in the size of families.

"Christianity thus checks population through prosperity and happiness and enlargement. Thus Christianity ultimately cures the evil of overpopulation in a most happy way. While the earliest effect of Christian activities is indeed to save populations from starvation and pestilence, their full effect utterly corrects any threat to over-population."

The title of this book seems too subtle. We suggest that a more informative one would have been *Rotary-Kiwanian Fundamentalism, approved by George F. Babbitt and Elmer Gantry.*

THE WAR ON MODERN SCIENCE. *A Short History of the Fundamentalist Attacks on Evolution and Modernism.*
By Maynard Shipley. *Alfred A. Knopf, Inc.*
$3.00 5½ x 8¼; xiv + 415 *New York*

Mr. Shipley is president of the Science League of America, a body organized to fight Fundamentalism. This book is intended as a history of the progress of the campaign during the past five years, and, one must suppose, as insidious propaganda against the palaeobaptists. How much good it will do in the latter direction seems dubious. Obviously no Fundamentalist is going to alter his views as a result of reading it. Those who are not Fundamentalists need no converting. The real usefulness of the book in the long run will be as a well put together contemporary record of an ephemeral social disturbance in American life, more idiotic perhaps than most, but on that very account the more certain to be short lived. We wish Mr. Shipley all success in the good fight he is making to hasten the final interment.

THE ORIGIN OF SPECIES BY MEANS OF NATURAL SELECTION *or the Preservation of Favored Races in the Struggle for Life.*
By Charles Darwin. *The Macmillan Co.*
80 cents (cloth) *New York*
4¾ x 7⅛; xxxv + 557

A cheap, but good reprint of the sixth edition of the great classic of biology, with an interesting introduction by Professor Edmund B. Wilson.

GENETICS

SEGREGATION AND AUTOGAMY IN BACTERIA. *A Contribution to Cellular Biology.*
By F. H. Stewart. *Adlard and Son, Ltd.*
7s. 6d. 5½ x 8½; v + 104 + 4 plates *London*
(paper)

This book is the record of an interesting piece of research, which leads the author to a new theory of the life-cycle and of the origin of variation in bacteria.

If a bacterium

"is placed in new surroundings with sufficient food it multiplies quickly by simple fission (colony formation). This vegetative phase is stopped by an intrinsic force, but it can be either lengthened or shortened by external conditions (amount of food available, moisture, crowding) and it can be continued indefinitely by frequent change of surroundings.

"Shortly before vegetative growth stops the second phase of the life-cycle begins, in which a few out of the great number of bacteria in a colony (either on solid or in liquid nidus) go through segregation, autogamic conjugation, and, under certain circumstances, variation. In spore-bearing races the zygote forms the spore. Segregation in bacteria is the same as in the higher forms; in it allelomorphic couples of the organism divide. We know little about the mechanism of autogamy, but it seems not unlikely that before segregation takes place each allelomorphic couple is represented in the 'anterior' and 'posterior' halves of the bacterium (Schaudinn and Dobell's pre-sporing division), and that, after segregation, and if nothing disturbs them, the 'right hand' allelomorphs of one half of the body unite with the 'left hand' allelomorphs of the other. At least this is as good a mental picture as any other. But, if a definite external stimulus is at the moment bearing on a heterozygous bacterium, then in the one pair (anterior and posterior) of allelomorphic couples which is concerned with the stimulus, the dominant allelomorphs are dissipated (as primitive polar bodies?), the recessives come together, and the bacterium varies.

"The recessive so formed may also vary in simple fission if one of its recessive allelomorphs is not pure but is loaded with a fragment of the dominant factor. It may then vary in two directions—by increasing, or decreasing, this fragment."

TILLOTSONS DIRECTORY OF PEDIGREE STOCK BREEDERS AND YEAR BOOK OF THE BREEDING INDUSTRY. *An Index of Pedigree Stock Breeders and Owners in England, Wales, Scotland, Ireland, and the Channel Islands; Australia, New Zealand, British South Africa and Canada; and Year Book Concerning Breeds and Events in the Breeding Industry in Various Countries.*
Compiled and Edited by R. de Toll.
Tillotsons Publishing Co.
£1. 15s. $7\frac{1}{4}$ x $8\frac{3}{4}$; 812 *London*

The general scope of this useful work is sufficiently indicated by its title. Some of the numerous special articles in the volume are of real interest and value to the student of genetics, as are also the excellent photographic illustrations of breed types. It is a pity that the live-stock industry of this country has no annual of similar scope.

GENETICS IN RELATION TO AGRICULTURE.
By Ernest B. Babcock and Roy E. Clausen.
McGraw-Hill Book Co., Inc.
$5.00 $5\frac{3}{4}$ x 9; xiv + 673 *New York*

This is the second edition, revised nearly to the point of complete rewriting, of what has come to be regarded as, on the whole, the best existing text book of genetics for teaching purposes. Its high reputation will be enhanced by its present form.

LE PROBLÈME DES TRANSFORMATIONS DES ÊTRES VIVANTS RÉSOLU EXPÉRIMENTALEMENT. *La mutation provoquée. Le mécanisme des mutations spontanées. La variabilité héréditaire des individus et la fixité des espèces. Nouvelles données de philosophie scientifique.*
By L. Rémy. *Gaston Doin et Cie*
10 francs $4\frac{1}{2}$ x 7; vii + 162 (paper) *Paris*

Mademoiselle Rémy furnishes in this book a brief, popular *résumé* of some of the elementary facts of modern genetics, Mendelian, mutation, etc. The results of some crossing experiments with peas are presented.

GENERAL BIOLOGY

INSTINCT IN THE CELL AND ORGANISM. *A Genetic Account of the Primal Urges, Impulses and Reactivities of Living Organisms. With Special Reference to the Evolutionary Development of the Human Psychic Life. In three Parts: I. The Instinctive Functionings of the Cell. II. The Genetic Development of the Psychic Powers. III. Instinct in the Development of the Social Life.*
By Neander P. Cook. *The Weimer Press*
$5.00 6 x $9\frac{1}{2}$; xii + 244 *Alhambra, Calif.*

We are told in a four page abstract (sold for 10 cents) which accompanies this book that: "Probably no book of recent years contains such far-reaching new conceptions of fundamental importance in Biology." This naturally suggests turning the book over to Reginald the Office Boy for his tender ministrations. But before doing so we took the trouble to read it. As a result we are not quite so sure that the bold asseveration quoted has not got some element of truth in it. The author seems clearly to fall under Augustus DeMorgan's definition of a paradoxer. But if one neglects certain developments of the

theory as unnecessary and unsupported by any established biological facts, the residue is an interesting speculation with much to commend it to the attention of biologists. The central idea is that: "Instinctive reactivity, instinctive responses, instinctive urges, these are the moving impulses in living beings, whether we study them as unicellulars, as plants or animals, as lone hunters or in armies, as swarms, flocks, herds, hives, peoples or nations." Space is lacking here to show how this idea is developed. It must suffice to say that while perhaps no qualified biologist will agree with Mr. Cook at all points it will do none of them any harm to read what he has to say.

POULTRY PRODUCTION.
By William A. Lippincott. Lea and Febiger
$3.50 5¼ x 7¾; viii + 602 *Philadelphia*

The fourth edition, thoroughly revised, of a standard poultry text. It is one of the most scholarly books in the field, extensively illustrated, and well documented with a bibliography covering 20 pages of closely set 8-point type. The general biologist will find it a useful *résumé* of the considerable contributions which have been made by poultry workers during the last 25 years to the knowledge of avian physiology and genetics.

REGENERATION UND TRANSPLANTATION. *1. Band: Regeneration.*
By E. Korschelt. Gebrüder Borntraeger
M.60 6½ x 10; xii + 818 (paper) *Berlin*

This is a colossal survey of the field of regeneration, thorough and systematic, as would be expected from its distinguished author. It is to be followed by a volume on transplantation and explantation, which is now in preparation. The painstaking thoroughness of the work is indicated by the fact that this first volume contains a bibliography covering 65 closely printed pages. The whole treatise will constitute a reference work which no biological laboratory can afford to be without.

FOUNDATIONS OF BIOLOGY.
By Lorande Loss Woodruff. The Macmillan Co.
$2.50 5 x 7¾; xxiii + 546 *New York*

MANUAL OF BIOLOGICAL FORMS.
By George A. Baitsell. The Macmillan Co.
$3.50 5 x 7¾; xiv + 411 *New York*

The first of these volumes is the third edition, revised, of a widely used textbook of elementary general biology. The chief addition to this new edition is a chapter on biology in relation to human welfare.

Dr. Baitsell has also revised his text, which is intended to serve as a complementary work to Professor Woodruff's. It gives detailed descriptions and directions for study of the forms used in laboratory work in general biology.

The two books together furnish the basis of an excellent course.

GENERAL BIOLOGY. *A Book of Outlines and Practical Studies for the General Student.*
By James G. Needham.
American Viewpoint Society, Inc.
$2.50 5¼ x 7½; xiv + 546 *New York*

The thirteenth edition of a standard and valuable text book. Professor Needham writes with a clarity, charm, and insight, rarely achieved by scientific men. These qualities are exhibited in high degree in this book as well as in his well-known text book of limnology *The Life of Inland Waters.*

THE MICROSCOPY OF DRINKING WATER.
By George Chandler Whipple. Revised by Gordon M. Fair and Melville C. Whipple.
John Wiley and Sons, Inc.
$7.00 *New York*
5¾ x 9; xix + 586 + 19 plates

A fourth edition, revised after the distinguished author's death by two of his colleagues, of a book which has been a standard reference work for sanitary engineers and limnologists for nearly thirty years. A large amount of new material has been added throughout the book, and it has been brought up to date. It thus starts another long career of usefulness.

PHEASANT JUNGLES.
By William Beebe. *G. P. Putnam's Sons*
$3.00 6 x 8¾; xiii + 248 *New York*

For the material of this popular travel book the author draws on his experiences of a number of years ago in the jungles of Ceylon, Borneo, the Malay Peninsula, and the Himalayas, when he was collecting material for his monograph on the pheasants. The tale has all the charm of style and thrilling interest of matter which the public has come to associate with Mr. Beebe's writings on natural history.

MICROSCOPIC FRESH WATER LIFE.
By F. J. W. Plaskitt.
Chapman and Hall, Ltd.
13s. 6d. 5¼ x 8¼; xi + 278 *London*

An elementary manual primarily intended for, and likely to be chiefly useful to, the amateur microscopist. It is abundantly illustrated, partly by photographs and partly by line drawings. The former are, on the whole, better executed than the latter.

HOW BIRDS LIVE. *A Brief Account of Bird Life in the Light of Modern Observation.*
By E. M. Nicholson.
Williams and Norgate, Ltd.
3s. 6d. 4¾ x 7¼; x + 139 *London*

A very interesting popular account of the natural history of common birds, with a number of valuable original observations on bird populations, natural elimination, and other ecological topics. We highly recommend this little book to the attention of general biologists and students of evolution.

KINETIC THEORY OF GASES.
By Leonard B. Loeb.
McGraw-Hill Book Co., Inc.
$5.50 5¾ x 9; xvi + 555 *New York*

A thorough, critical review of the present state of knowledge and opinion regarding the kinetic theory of gases. It is primarily intended for students of physics and chemistry, but will be a useful reference work for general biologists and physiologists. It is abundantly documented bibliographically, and has good indices.

DAS LEBEN IN FINALER AUFFASSUNG. *Abhandlungen zur theoretischen Biologie, Heft 26.*
By Eugenio Rignano. Authorized German edition by Paul Graf Thun-Hohenstein.
Gebrüder Borntraeger
2.70 marks 6½ x 10; 35 (paper) *Berlin*

A German translation of a condensed statement of the author's well known vitalistic theory of the observed teleology in nature, with an introduction by Hans Driesch, saying, in effect, that while Rignano's brand of vitalism is not his brand, still all vitalism is good, and urging the reader to compare the two kinds.

THE LAWS OF LIVING THINGS.
By Edward J. Menge.
The Bruce Publishing Co.
$1.72 5¼ x 7¾; 530 *Milwaukee*

A high-school textbook of biology, which starts off with the perch as the standard type form, on which the discussion of other living things is hung. The book is extremely comprehensive though elementary.

HUMAN BIOLOGY

THE MOTHERS. *A Study of the Origins of Sentiments and Institutions.*
By Robert Briffault. *The Macmillan Co.*
$27.00 *New York*
6 x 9⅞; Vol. I, xix + 781
II, xx + 789
III, xv + 841

This is a monumental and brilliant contribution to prehistory. The method is to re-examine the data available regarding the ethnography of primitive races of mankind, and from it synthetically to reconstruct the probable course of human social evolution from its earliest stages. The material which Mr. Briffault uses is old, and available to everyone. But what a thorough and critical combing-over he has given it! His contribution, apart from the colossal industry which the work has involved, is a fresh point of view. It is that: "The social characters of the human mind are, one and all, traceable to the operation of instincts that are related to the functions of the female and not to those of the male. That the mind of women should have exercised so fundamental an influence upon human development in the conditions of historical patriarchal societies is inconceivable. I was thus led to reconsider the early development of human society, of its fundamental institutions and traditions, in the light of the matriarchal theory of social evolution."

The author is thoroughly convinced of the overwhelming importance of sex in social life. And in prehistoric stages of culture he makes a very strong case that the interests and viewpoints of women played a much more important rôle than in any society now existing. The final conclusion reached is that: "The traditional inheritance of the human mind, if these considerations are well founded, has been moulded in the first instance not by the fierce passions of wild hunters battling for the possession of food and of women, but by the instincts of the mothers."

Every serious student of human biology should have this work on his shelves. Besides the intrinsic value of its contribution it is a reference work of first importance.

ARABIAN SOCIETY AT THE TIME OF MUHAMMAD. *Parts I and II.*
By Pringle Kennedy. *Thacker, Spink and Co.*
Rs. 7/8 5¼ x 8½; vi + 253 *Calcutta*

This is an extremely interesting contribution to human biology. The point of view from which the analysis of the early history of Muhammadanism is undertaken is indicated by the following quotation:

"Whatever the opinion one may have of this extraordinary man, whether it be that of the devout Muhammadan, who considers him the last and greatest herald of God's word, or of the fanatical Christian of former days, who considers him an emissary of the Evil one, or of certain modern Orientalists, who look on him rather as a politician than a saint, as an organizer of Asia in general, and Arabia in particular, against Europe, rather than as a religious reformer; there can be no difference as to the immensity of the effect which his life has had on the history of the world. To those of us, to whom the man is everything, the milieu but little, he is the

supreme instance of what can be done by one man. Even others, who hold that the conditions of time and place, the surroundings of every sort, the capacity of receptivity of the human mind, have, more than any individual effort, brought about the great steps in the world's history, cannot well deny, that even if this step were to come, without Muhammad, it would have been indefinitely delayed."

The book contains much matter of great interest to the sociologist, the psychologist, and the eugenist, as well as to the historian *sensu stricto*. It is interesting to learn, for example, that none of the sons of the first three Caliphs, Abu Bakr, Omar, and Othman, all of whom were indeed superior persons, "inherited their father's character."

THE HUMAN BODY.
By Logan Clendening. Alfred A. Knopf, Inc.
$5.00 6 x 9¼; xxii + 399 *New York*
THE HUMAN BODY.
By Trevor Heaton. E. P. Dutton and Co.
$3.00 5½ x 8; ix + 250 *New York*

These two books with the same title appear almost simultaneously, the first by an American practising physician, the second by an Oxford don. Both are sound, authoritative, well-written treatises intended to give the layman a clear and sufficient understanding of how his body is put together and how it works in health and in disease. Both serve this purpose incomparably better than any prior books in the field. They make both the old-fashioned "family doctor book" and the high-school "physiology and hygiene" look the sad, dull things that they were.

So far the two books travel along together. Then their paths begin to diverge. Dr. Clendening's book is vastly more entertaining, better and more extensively illustrated, and written with a Gargantuan dash, vigor, wit, and humor which leaves it with no real competitor whatever. He explodes ruthlessly all the popular superstitions about the body and its care which have held sway over the lay mind, and only in lesser degree over a good fraction of the collective medical mind, for many long ages. Altogether, Dr. Clendening has made a notable contribution to the joy of the world as well as to the store of common knowledge. His book will irritate the pedants and the uplifters, in and out of the medical profession, but we see no harm in that.

POPULATION PROBLEMS OF THE AGE OF MALTHUS.
By G. Talbot Griffith. The Macmillan Co.
$5.00 5½ x 8¾; 276 *New York*

In this extremely interesting and useful volume the author has attempted to reconstruct for modern eyes the statistical picture which Malthus had before him when he wrote his essay.

"This theory that an increasing population was in all cases desirable and necessary became an axiom which continued for some centuries, and discussions were always taking place as to the various means of securing this. Towards the end of the eighteenth century, when, in point of fact, the population was increasing with a rapidity hitherto unapproached, there was, owing largely to the failure to take a Census, a great feeling that the population was decreasing.

"It was into such an atmosphere that Malthus's *Essay on Population* burst. The continued absence of any reliable and official figures of the population heightened the surprise effect of the essay, and when in 1801 a Census was taken, it confirmed what Malthus had said about the increase of the population up to that time. The *Essay*, backed up by the Census, killed the axiom that under all circumstances an increasing population is desirable."

The book is a valuable contribution to the history of human biology.

DIE MESTIZEN AUF KISAR.
By Ernst Rodenwaldt. *G. Kolff and Co.*
I, xvii + 483 *Weltevreden*
II, tables and plates

This is a contribution of the very first importance to the research literature of human biology. It is a thorough, detailed, and comprehensive study of the anthropology, biology, and sociology of the European-native bastard people of Kisar, a small island in the so-called "Southwest Islands" group in the Dutch East Indies. The nearest large island is Timor. About the middle of the 17th century the Dutch took up residence on the island. The descendants of the original crosses between these Europeans and the natives inhabit the island today. They have been studied, family by family, in the most exhaustive manner by Dr. Rodenwaldt. One volume of the work is devoted to plates and pedigree charts. We congratulate the author on so fine a piece of work, and commend it to all students of human biology.

THE MYSTIC ROSE. *A Study of Primitive Marriage and of Primitive Thought in its Bearing on Marriage.*
By Ernest Crawley. Revised by Theodore Besterman. *Boni and Liveright*
$10 Vol. I, 5½ x 8½; xx + 375 *New York*
Vol. II, viii + 340

The original edition of this classic of ethnology has long been out of print. The material for this welcome reissue was to some extent revised by Mr. Besterman after the author's death, but mainly augmented by additions, consisting chiefly "first, of evidence, or further evidence, where the argument seemed to require strengthening, and of specimens of the large accumulations of anthropological material during the last two decades, and, secondly, of replies to criticisms and of discussions of the more recently advanced theories." There has also been added a bibliography covering 42 pages, and the index has been made more comprehensive and detailed. It is a real service to human biology to have made this treatise once more readily available.

CHILD LIFE INVESTIGATIONS. *Social Conditions and Acute Rheumatism. Medical Research Council Special Report Series, No. 114.*
By G. F. Still (and a Committee).
His Majesty's Stationery Office
2s. 6d. 6 x 9¾; 108 (paper) *London*

The general conclusion reached from this painstaking study of the environmental influences in relation to the incidence of acute rheumatism in children is: "That although it is difficult to point to this or that fault of environment as responsible for rheumatism, nevertheless it is by raising the standard of environment, improving the home conditions so that they approximate to the well-ordered conditions found in such institutions as those in which rheumatism was found to be much less common, and probably by reducing crowding, so that the possibility of contagion may be diminished, that we may hope to reduce the frequency of rheumatism in children."

THE ETHICS AND ECONOMICS OF FAMILY ENDOWMENT. *The Social Service Lecture, 1927.*
By Eleanor R. Rathbone. *The Epworth Press*
2s. 6d. net 5¼ x 8; 118 *London*

The central thesis of this tract, delivered as an endowed lecture to the Wesleyan Conference, is that society as a whole should encourage the indigent, impoverished, and generally submerged portion of the population to have as many children

as they like, by the simple and efficient expedient of removing, at the public expense, any economic burden incident to rearing large families. This proposal is seriously made, and in the name of Christianity, by a women who is herself a citizen of a country in which the population increases by about 600 a day and in which something of the order of a million people are at all times unable to find work to keep themselves alive. We like the nerve of the proposal, but not much else about it.

THE END OF A WORLD.
By Claude Anet. Translated from the French by Jeffery E. Jeffery. Alfred A. Knopf, Inc.
$3.00 5 x 7½; 268 *New York*

An entertaining romance, which attempts to portray through the medium of fiction the end of the prehistoric civilization which had its metropolis in what is now Les Eyzies. It is charmingly written. Some of the reconstructions of this lost civilization which the author imagines are plausible and seem probably true. Others are more dubious. It is almost certain that as more evidence accumulates some of the theories about the Solutrean and Aurignacian civilizations now prevailing in the best archeological circles will be modified. The book is illustrated with bold and rather effective black and white drawings from cave paintings and sculptures.

MAORI SYMBOLISM. *Being an Account of the Origin, Migration, and Culture of the New Zealand Maori as Recorded in Certain Sacred Legends.*
By Ettie A. Rout. Harcourt, Brace and Co.
$6.00 6 x 9¼; xxxii + 322 *New York*

Ettie Rout can be depended on to write vividly of whatever subject she tackles. This book has obviously been produced *con amore*. The dedication is to "my fellow-countrymen—the New Zealand Maori." It is a detailed, rather rambling, but extremely interesting discussion of Maori ethnology and folklore, based upon evidence given by "an Arawa Noble," Hohepa Te Rake. The material is discussed under five main heads: Origin and migration of the New Zealand Maori; health and race culture; social organization; agriculture and building; sacred life symbols. The book is extensively and well illustrated, and has a detailed index.

MENSCHLICHE ERBLICHKEITSLEHRE UND RASSENHYGIENE. *Band I. Menschliche Erblichkeitslehre.*
By Erwin Baur, Eugen Fischer, and Fritz Lenz. J. F. Lehmanns Verlag
16 Mk. 6 x 9; xii + 601 *München*

The third, revised and enlarged, edition of the best existing general book on human inheritance. The authors express the belief that not only has general genetic theory become stabilized but also human genetics, so that future editions of this book are not likely to require fundamental revision. It is a pity that we have in English no such sound, comprehensive, and stimulating work as this on human heredity.

THE PRINCIPLES AND PRACTICE OF MEDICINE. *Designed for the Use of Practitioners and Students of Medicine.*
By Sir William Osler. Tenth Edition, Thoroughly Revised by Thomas McCrae. D. Appleton and Co.
$7.50 6 x 9; xxviii + 1233 *New York*

The "one volume Osler" is a classic of medical literature. It is full of the wisdom of "the Chief." Dr. McCrae is a

careful and conservative editor. In his preface to this tenth edition he quotes Osler's saying that "A Textbook is not a Year-Book," and says that he has endeavored to "retain the features characteristic of Sir William Osler." It is a great book and will long continue its useful service. For the human biologist who wants to find, in brief space, what is known about a particular disease and its treatment there is no better source than this.

IMMIGRANTS AND THEIR CHILDREN 1920. *A Study Based on Census Statistics Relative to the Foreign Born and the Native Whites of Foreign or Mixed Parentage. Census Monographs VII.*
By Niles Carpenter.
Government Printing Office
$1.50 6¾ x 10; xvi + 431 *Washington*

An analysis of the population and birth data of 1920 relative to racial origins. The study follows lines somewhat similar to those of Pearl in his "Vitality of the Peoples of America," and confirms his principal conclusions. But this investigation is more comprehensive in its scope. It is done with critical care and deserves the attention of all students of human biology.

THE ANGLO-SAXONS IN ENGLAND *During the Early Centuries After the Invasion.*
By Nils Aberg. *W. Heffer and Sons, Ltd.*
12s. 6d. *Cambridge*
6½ x 10; vii + 219 (paper)

An interesting, finely printed and illustrated treatise on Anglo-Saxon archeology, based largely upon English museum collections of metal artefacts.

TRENDS OF POPULATION IN THE REGION OF CHICAGO.
By Helen R. Jeter.
The University of Chicago Press
$2.50 8½ x 11; xv + 64 *Chicago*

This is a detailed statistical study, with numerous graphs, of the growth of the population of Chicago and surrounding urban and rural areas. The study was made for the Chicago Regional Planning Association. Predictions of future population up to 1950 are included.

ALLGEMEINE KONSTITUTIONS-LEHRE *in Naturwissenschaftlicher und Medizinischer Betrachtung.*
By O. Naegeli. *Julius Springer*
Rm. 9.60 *Berlin*
6¼ x 9½; iii + 118 (paper)

A brief but comprehensive review of human genetics and the constitutional factors in disease. The book will be found useful by the medical student or practitioner who cannot give the time necessary for the perusal of Bauer's standard work on the subject.

EVOLUTION OF PREVENTIVE MEDICINE.
By Sir Arthur Newsholme.
Williams & Wilkins Co.
$3.00 5 x 7¼; xv + 226 *Baltimore*

A brief outline, illustrated with portraits, of the history of public health and preventive medicine. The book would have been more useful to the serious student if there had been included a bibliography giving precise citations to the sources used.

ZOOLOGY

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferungen VI, VII, VIII, IX.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft M. B. H. *Leipzig*

Lieferung VI, M. 16.80
6 x 8½; 212 (paper)
Lieferung VII, M. 10.80
6 x 8½; 136 (paper)
Lieferung VIII, M. 14.60
6 x 8½; 186 (paper)
Lieferung IX, M. 13.60
6 x 8½; 146 (paper)

These four parts maintain well the standard set in earlier numbers of this collective work on the fauna of the North and Baltic Seas, which have already been noticed in THE QUARTERLY REVIEW OF BIOLOGY as they appeared. The groups discussed in these numbers are as follows: *Epicaridea*, by F. Nierstrasz and G. A. Brender à Brandis; *Stomatopoda* and *Decapoda*, by H. Balss; *Gadiformes* and *Cyclostomi*, by W. Schnakenbeck; *Ctenophora*, by T. Krumbach; *Leptostraca*, by J. Thiele; *Elasmobranchii* and *Chondrostei*, by E. Ehrenbaum; *Tintinnidae*, by E. Jörgensen; non-parasitic *Copepoda*, by O. Pesta; *Cirripedia*, by P. Krüger; *Branchiostoma*, by V. Franz; *Oligochaeta*, by W. Michaelsen; *Thaliacea*, by J. E. W. Ihle; *Teleostei Physostomi*, by H. M. Kyle and E. Ehrenbaum.

L'INFECTION MICROBIENNE ET L'IMMUNITÉ CHEZ LA MITE DES ABEILLES, *Galleria mellonella.*
By S. Métalnikov. *Masson et Cie*
18 francs 6½ x 10; 139 (paper) *Paris*

This is an extremely interesting monograph on the wax moth (*Galleria*), which seems likely to become a useful laboratory animal. Perhaps the most interesting biological peculiarity of this odd animal is its ability to digest beeswax, and utilize it as its chief source of nourishment. The principal object of the monograph is the study of immunity in *Galleria*. Acquired immunity is easily obtained, and is stated to be transmissible to succeeding generations. As might be expected *Galleria* is able to digest easily the waxy envelope of the tubercle bacillus. This fact opens up some interesting possibilities of research. Biologists will want to read this monograph, even though they are not primarily interested in the special problems of immunity.

REPORT ON CETACEA STRANDED ON THE BRITISH COASTS FROM 1913 TO 1926.
By Sir S. F. Harmer.
British Museum (Natural History)
7s. 6d. *London*
9¼ x 12; 91 + 7 maps (paper)

This is the author's tenth, and last, report in an interesting series, which has contributed much to knowledge of the Cetacea. While primarily having to do with stranded whales this present report amounts to a general discussion of the biology of Cetacea. For the specialist the principal result is "the record of the seasonal and local occurrences of the several species, each of which has definite partialities as to time and place. Stranded specimens cannot indeed be expected to give full information on these subjects, but it is found that each year examined gives on the whole the same results as its predecessors, and the evidence thus obtained need not be ignored."

The report is rather fully illustrated, and contains a key for the determination of British whales and dolphins and a short bibliography.

HOST-PARASITE RELATIONS BETWEEN MAN AND HIS INTESTINAL PROTOZOA.

By Robert Hegner. *The Century Company*

$3.50 5¾ x 8¾; xiii + 231 *New York*

This is the first volume in the Century Biological Series, of which Dr. Hegner is general editor. The purpose of the book is "to gather together the more relevant data regarding the host-parasite relations of the intestinal protozoa of man and to present them in logical order in such a way as to bring out the state of our knowledge with special reference to the desirability of further studies." The treatment is excellent, but there is a sparseness of illustrations for which there seems no compelling reason. There is a bibliography of 25 pages, and author and subject indices. We extend a hearty welcome to the series which this volume inaugurates at a high level of excellence.

ECONOMIC BIOLOGY FOR STUDENTS OF SOCIAL SCIENCE. *Part I. Harmful and Useful Animals.*

By Philippa C. Esdaile.

University of London Press

7*s. 6d.* 5½ x 8½; xv + 175 *London*

Specialization goes ever further and finer. Here we have an elementary zoology for students of what we call in this country "domestic science." It picks out for description and illustration (both excellent) those animals and plants "which are, or may be, closely associated with man and his household." The present Part I deals with animals, such as bath sponges, pin-worms, bed bugs, cockroaches, spiders, etc. Part II will discuss "Animal and Vegetable Products." The book should serve extremely well the class for which it is intended. And furthermore every householder will find it an interesting book to have about.

SEASHORE ANIMALS OF THE PACIFIC COAST.

By Myrtle R. Johnson and Harry J. Snook.

The Macmillan Co.

$7.50 6 x 9½; xiv + 659 *New York*

This stately and beautifully illustrated volume is intended to furnish those interested in natural history, whether professionally or as amateurs, with non-technical accounts of the structure and habits of the common seashore animals of the west coast of North America. The arrangement of the book is according to the taxonomic series. It covers only the invertebrates, with a short final chapter on the Chordata. It is very well done, and will have an even wider field of usefulness than that contemplated in its plan. There is a bibliography of 14 pages, a glossary, and a detailed index.

REPTILES AND AMPHIBIANS. *Their Habits and Adaptations.*

By Thomas Barbour. *Houghton Mifflin Co.*

$3.50 5½ x 9; xx + 125 *Boston*

This is a popular, but at the same time soundly scientific treatise on reptiles and amphibians, with special emphasis on their ecology, habits, and behavior. It is beautifully and extensively illustrated, contains a short selected bibliography, and is well indexed. It is an example of the highest type of popular natural history writing. A part of the material was used as a series of Lowell Lectures.

GENERAL CATALOGUE OF THE HEMIPTERA. *Fascicle I. Membracidae.*

By W. D. Funkhouser. *Smith College.*

$3.60 *Northampton, Mass.*

6 x 9; ix + 581 (paper)

This is the first part of an ambitious undertaking, which will be of great value

when completed to all entomologists, and particularly to hemipterologists. The general editor is Dr. G. Horváth, of the Museum at Budapest, and Prof. H. M. Parshley of Smith College is the managing editor. This first fascicle is devoted to the synonomy of the Membracidae, with indications as to the historical development of the knowledge of each species, and as to its geographical distribution.

THE PRACTICAL VALUE OF BIRDS.
By Junius Henderson. *The Macmillan Co.*
$2.50 5¼ x 7¾; xii + 342 *New York*

The author is the professor of natural history at the University of Colorado. The book is a detailed, fully documented presentation of the data of economic ornithology, based largely upon the examination of the stomach contents of North American birds. It is a valuable contribution to the literature of natural history.

TEXTBOOK OF GENERAL ZOOLOGY.
By Winterton C. Curtis and Mary J. Guthrie.
John Wiley and Sons, Inc.
$3.75 5¾ x 9; xv + 585 *New York*

An excellent textbook of elementary zoology, which "represents a temporary crystallization of the course in General Zoology as developed in the University of Missouri." From a pedagogical viewpoint it is sound, well-knit, and practical. We predict for it a great success in its field.

GLIMPSES OF ANIMAL LIFE.
By Various Authors. *John Murray*
2s. 6d. 4¾ x 7¼; 184 *London*

A selection of quotations from the works of eight popular writers on natural history, the extracts being chosen "no less for the style" than for the information imparted. The result is a charming little book.

A LABORATORY COURSE IN GENERAL ZOÖLOGY. *A Guide to the Dissection and Comparative Study of Animals.*
By Henry S. Pratt. *Ginn and Co.*
$1.72 5½ x 8¼; x + 244 *Boston*

This is a revised edition of the author's well known "Course in Invertebrate Zoölogy" with two vertebrate, perch and frog, discussions added in simplified form from his "Course in Vertebrate Zoölogy."

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 242. Methoden zur Untersuchung parasitischer Würmer. Züchtung parasitischer Würmer.*
By W. A. Collier. *Urban und Schwarzenberg*
2.50 marks 7 x 10; 42 (paper) *Berlin*

A useful summary of technique for the parasitologist.

BOTANY

A TREATISE ON THE BRITISH FRESHWATER ALGAE.
By G. S. West. New and revised edition, in great part rewritten, by F. E. Fritsch.
The Macmillan Co.
$7.00 5½ x 8½; xv + 534 *New York*

This new edition of a standard systematic treatise on freshwater algae (and other pigmented Protophyta) will be found useful by all limnologists, and indeed general biologists. The revision has been thorough. There is much more extensive documentation of the literature than in the original edition. The keys for

the identification of the genera are excellently arranged. Sixty-two genera are included which were not in the earlier edition. Every British genus is figured. Altogether this is a valuable reference work.

NOTES SUR QUELQUES CAS DE TÉRATOLOGIE VÉGÉTALE. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 6.*
By Frère Marie-Victorin.
University of Montreal
25 cents *Montreal*
6 x 9; 7 + 1 plate (paper)

NOTES POUR SERVIR À L'HISTOIRE DE NOS CONNAISSANCES SUR LES ABIÉTACÉES DU QUÉBEC. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 7.*
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 24 + 3 plates (paper)

NOUVELLES ÉTUDES SUR LES COMPOSÉES DU QUÉBEC. *Contributions du Laboratoire de l'Université de Montréal, No. 8.*
By Frère Marie-Victorin.
University of Montreal
50 cents *Montreal*
6 x 9; 20 + 4 plates (paper)

Interesting contributions respectively to teratology and morphogenesis; the history of Canadian botany; and local distribution and ecology.

PLANT ECOLOGY.
By W. B. McDougall. *Lea and Febiger*
$3.00 *Philadelphia*
5¼ x 7¾; viii + 326

A well-written and extensively illustrated textbook for college and university classes in ecology. Each chapter is followed by a list of references for collateral reading, and at the end is a short chapter of suggestions to the teacher in arranging for laboratory and field work. An excellent text.

A TEXTBOOK OF BACTERIOLOGY. *A Treatise on the Application of Bacteriology and Immunology to the Etiology, Diagnosis, Specific Therapy and Prevention of Infectious Diseases, for Students and Practitioners of Medicine and Public Health.*
By Hans Zinsser (With a section on Pathogenic Protozoa, By E. E. Tyzzer).
D. Appleton and Co.
$7.50 6 x 9; xx + 1053 *New York*

The sixth edition, "rewritten, revised and reset" of a standard bacteriological text. The most important single alteration is a new section on parasitic protozoa by Prof. Tyzzer. In its new form this book will continue its long and deserved success.

THE BOTANY DRILL BOOK.
By H. G. Baker. *H. G. Baker*
Southwestern College, Winfield, Kans.
25 cents 3¾ x 6; 50 (paper)

A quiz compend, now in its second edition, containing 1000 questions and their answers, the latter consisting almost always of one word.

COTTON. *History, Species, Varieties, Morphology, Breeding, Culture, Diseases, Marketing, and Uses.*
By Harry Bates Brown.
McGraw-Hill Book Co., Inc.
$5.00 6¾ x 9; xi + 517 *New York*

The scope of this agricultural text is sufficiently indicated in the sub-title. It is a thorough piece of work and a valuable addition to botanical and agricultural literature.

MORPHOLOGY

ANATOMICAL, PHYLOGENETICAL AND CLINICAL STUDIES ON THE CENTRAL NERVOUS SYSTEM.
By B. Brouwer. *Williams & Wilkins Co.*
$2.50 5½ x 8½; 67 *Baltimore*

These three lectures on the Herter Foundation, by the distinguished professor of clinical neurology at Amsterdam, deal respectively with (a) the projection of the retina in the brain; (b) the pathology of sensibility; and (c) the significance of phylogenetic studies for the neurologist. A bibliography of the pertinent literature follows each lecture.

VERTEBRATE EMBRYOLOGY.
By Waldo Shumway.
John Wiley and Sons, Inc.
$3.75 5¾ x 9; viii + 314 *New York*

A textbook of embryology for undergraduates. The forms particularly discussed are *Amphioxus*, the frog, the chick, and the pig. The first two parts of the book give a general account of development. The third and fourth parts are guides for laboratory work. The book is well illustrated, chiefly by clear line diagrams.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 236. Methoden zur Untersuchung der Morphologie der Primaten.*
By Stefanie Oppenheim, Adolf Remane, and Wilhelm Gieseler. *Urban und Schwarzenberg*
9 marks 7 x 10; 151 (paper) *Berlin*

An extremely useful handbook of directions for the quantitative study of the morphology, particularly skeletal, of the primates. Workers wishing to make biometric studies on any mammal will find it helpful, because it indicates clearly the measurements which will be comparable to those used in modern anthropometry.

HISTOLOGICAL TECHNIQUE. *A Guide for Use in a Laboratory Course in Histology.*
By B. F. Kingsbury and O. A. Johannsen.
John Wiley and Sons, Inc.
$2.25 5¾ x 9; vii + 142 *New York*

A useful laboratory guide, in which the first author contributes the vertebrate technique and the second, the invertebrate (particularly entomological). There is a bibliography of 54 titles.

PHYSIOLOGY

CONDITIONED REFLEXES. *An Investigation of the Physiological Activity of the Cerebral Cortex.*
By I. P. Pavlov. Translated and edited by G. V. Anrep. *Oxford University Press*
$9.00 6¼ x 9½; xv + 430 *New York*

This book is an English translation, by one of Pavlov's old students, of a series of 24 lectures delivered in Petrograd in 1924, which had for its purpose to summarize in a systematic way all of the work that had been done in Pavlov's laboratory on the activities of the cerebral hemispheres of the dog, which researches had been going on for more than a quarter of a century. It scarcely needs saying that it is a great and significant service to biology, on the part of both author and translator, to have made this most important work available in a more widely known language than Russian. There is no attempt to review the literature outside of that from Pavlov's own laboratory.

The whole book is just a straightforward, single-tracked exposition of the results of a wisely planned research program, persistently and painstakingly followed through. It is a pity that there are not more books like this.

ASPECTS ACTUELS DE LA PHYSIOLOGIE DU MYOCARDE (*Première Série*). *L'onde d'excitation motrice, son origine, sa propagation, ses manifestations électriques.* *By Henri Fredericq*

Les Presses Universitaires de France

40 francs 6 x 9¼; viii + 300 *Paris*

A thorough review of the physiology of heart muscle, documented with a bibliography of 779 titles. The material is discussed under the following heads: The origin and the conduction within the heart of the excitation and the contraction; autonomous rhythms of the heart; neurogenic and myogenic theories of automatism and intracardiac conduction; the electrocardiogram from a physiologic point of view; the nature of the auricular and the ventricular systoles.

THE PHYSIOLOGY OF REPRODUCTION IN THE COW.

By John Hammond. *The Macmillan Co.*

$7.00 7 x 10; xvi + 226 *New York*

An interesting and valuable summary of the present state of knowledge of the physiology of reproduction and development of the udder in the cow, which includes a large amount of original data derived from the author's own investigations in these fields. It will be a first-order reference book for all students of agricultural physiology. There is a bibliography of 400 titles. The book is abundantly and beautifully illustrated, though in some cases, as for example Plate XX, the original photographic work could have been better done.

DIE UNREGELMÄSSIGE HERZTÄTIGKEIT.

By K. F. Wenckebach and Hch. Winterberg.

Wilhelm Engelmann

Leipzig

78 marks

Textband; 7 x 10; vii + 635

Tafelband; 7 x 10; 184 plates

This book started, in 1914, as a second edition of Wenckebach's treatise on the pathological physiology of the heart, but it was decided as the work progressed to rewrite practically the whole and make essentially a new work of it. In its new form it will constitute a basic reference work for the clinician and the student of pathological physiology. It is beautifully printed and illustrated. There is a bibliography of 1084 titles.

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome VII. Sang et lymphe. Réactions d'Immunité.*

By Ch. Achard, A. Besredka, Léon Binet, J. Besançon, J. Bordet, L. Cuénot, H. Delaunay, M. Doyon, R. Fabre, J. Jolly, Ph. Pagniez, G. H. Roger, F. Schulmann and P. Émile-Weil.

Masson et Cie

65 francs 6½ x 9½; xi + 502 *Paris*

TRAITÉ DE PHYSIOLOGIE NORMALE ET PATHOLOGIQUE. *Tome XI. Reproduction.*

By Léon Binet, H. Busquet, Ch. Champy, E. Lesné, A. Pézard, Ch. Porcher, E. Rabaud, H. Vignes.

Masson et Cie

65 francs 6½ x 9½; xi + 496 *Paris*

These parts of the eleven volume text book of physiology which is being pro-

duced by the cooperation of the leading French physiologists and general biologists will be found useful for reference by American workers, chiefly because they reflect so thoroughly the French literature and point of view in the fields covered. The second of the two volumes here noticed has the greater general biological interest. Particularly noteworthy in it are the articles by Prof. Pézard on secondary sexual characters and by Prof. Porcher on milk secretion. The article on heredity by Prof. Rabaud will be regarded as reactionary by most American geneticists.

THE FOUNDATIONS OF NUTRITION. *By Mary Swartz Rose.* *The Macmillan Co.*
$2.75 5 x 7½; xi + 501 *New York*

A popular book on diet, by the professor of nutrition at Teachers College, Columbia University, intended for "those who wish to live more intelligently." It is fully and rather well illustrated, and carries reference lists of literature after each chapter. Its viewpoint reflects that of the Columbia school of nutrition.

POTASSIUM AND TARTRATES. *A Review of the Literature on Their Physiological Effects.*
By Ralph W. Webster (With a Digest and Bibliography of the Literature, by W. A. Brennan). *The Commonwealth Press*
$2.50 5 x 7½; 168 *Chicago*

This is essentially an annotated bibliography of selected papers on the biological effects of potassium salts and of tartrates. While nothing is overtly said about it, we suspect that the underlying purpose of this treatise is that of propaganda in the baking powder war now on between Battling Alum of Chicago, and The Cream of Tartar Kid of New York.

THE METABOLISM OF THE FASTING STEER. *Carnegie Institution of Washington Publication No. 377.*
By Francis G. Benedict and Ernest G. Ritzman *Carnegie Institution of Washington*
$2.50 *Washington, D. C.*
6¾ x 10; viii + 246 (paper)

A detailed investigation of the metabolism chiefly of two steers, which were subjected at various intervals during two and one-half years to seven fasting periods of from 5 to 14 days in duration. The results are too manifold and detailed for brief summary here.

RECENT ADVANCES IN HAEMATOLOGY.
By A. Piney *P. Blakiston's Son and Co.*
$3.50 5¼ x 8; viii + 276 *Philadelphia*

A useful contribution to the "Recent Advances Series," but of greater interest to the medical man than to the general biologist. The chapter on "Haemorrhagic Diatheses" will interest the human geneticist.

LEITFADEN ZU TIERPHYSIOLOGISCHEN ÜBUNGEN.
By Paul Krüger. *Gebrüder Borntraeger*
M. 3 5½ x 8¾; viii + 92 *Berlin*

A laboratory guide for a course in general physiology, by the *a. o.* Professor of Zoology and Comparative Anatomy at the University of Berlin.

PERMEABILITÄTSSTUDIEN AN EINER ÜBERLEBENDEN MEMBRAN.
By Ernst Wertheimer.
Urban und Schwarzenberg
2.40 marks 7 x 10; 25 (paper) *Berlin*

An account of an interesting series of investigations on permeability, made with

the surviving skin of a frog's leg as the membrane. The brochure constitutes the second number in the new series of *Fortschritte der naturwissenschaftlichen Forschung* edited by Professor Abderhalden.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 227.* Containing the following articles: *Unsere Methoden zur graphischen Bestimmung des Gesamtgaswechsels*, by J. G. Dusser de Barenne and G. C. E. Burger; *Die Bestimmung des Blutgaswechsels einzelner Organe*, by Friedrich Verzár; *Stoffwechselversuch am Menschen und am Hunde*, by Robert E. Mark.

Urban und Schwarzenberg
7.80 marks 7 x 10; 124 (paper) *Berlin*

Lieferung 234. Containing the following articles: *Diazotieren*, by Siegfried Edlbacher, and *Ätzalkalischmelze Nitrieren*, by Ernst Maschmann.

Urban und Schwarzenberg
10 marks 7 x 10; 185 (paper) *Berlin*

Lieferung 237. Alkylieren.
By Josef Halberkann.

Urban und Schwarzenberg
12 marks 7 x 10; 220 (paper) *Berlin*

Lieferung 240. Acylieren. Acetalieren.
By Josef Halberkann.

Urban und Schwarzenberg
16 marks 7 x 10; 276 (paper) *Berlin*

Lieferung 243. Containing the following articles: *Biochemische Methoden auf dem Gebiete der Pflanzenhygiene*, by Julius Stoklasa, and *Die Phytochemie als Hilfsmittel zur Lösung phylogenetischer Fragen*, by Hermann Thoms.

Urban und Schwarzenberg
7 marks 7 x 10; 132 (paper) *Berlin*

These numbers of the Abderhalden handbook deal with various aspects of pure and applied biochemistry, and maintain well the high standard set in previous parts. The last paper listed, by Thoms, has considerable general biological interest.

THE CLINICAL INTERPRETATION OF BLOOD CHEMISTRY.
By Robert A. Kilduffe. *Lea and Febiger*
$2.50 5¼ x 7¾; x + 186 *Philadelphia*

The purpose of this book is to furnish the practising physician with the necessary background to enable him to understand the significance of the findings of the laboratory man regarding the blood chemistry of his patients, particularly diabetics and nephritics. The compiling and editing are well done.

DIGEST OF ELEMENTARY CHEMISTRY.
By Martin Mendel. *Globe Book Co.*
67c 5 x 7¼; v + 234 *New York*

A quiz compend of chemistry for high school students.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen, für Studierende, Ärzte, Biologen und Chemiker. II. Band: Stoffwechsellehre. IV. Lieferung: Eiweissstoffwechsel. Vorlesung: XLI Bis LI.*
By Otto Fürth. *F. C. W. Vogel*
Marks 15 *Leipzig*
7 x 10; iv + 148 (paper)

The topics treated in this part of the Fürth textbook of physiological chemistry, already noticed in THE QUARTERLY REVIEW OF BIOLOGY, are: Introduction to the theory of metabolism; protein diges-

tion in the stomach; protein digestion in the intestine; protein synthesis in the organism; proteolytic and peptolytic ferments; uric acid; hippuric acid; creatin and creatinin; oxyproteic acids; the fate of cyclic complexes of the protein molecule in the organism; haemoglobin excretion.

SEX

THE WOMAN A MAN MARRIES
By Victor C. Pedersen. George H. Doran Co.
$3.00 5¾ x 8½; x + 276 *New York*

This is a realistic and mostly sound discussion of sex relations in married life by a physician. The point of view is to

"treat of ignorance of biology and physiology, of social development and social conditions, of marriage, of venereal disease, and of the restoration or relief of the whole complex difficulty as fully as possible and as minutely as is wise for the purpose. Despite research and reading for many years in this field, I know of no other work which examines or aims to examine the relation of the so-called virtuous woman to the whole sexual problem. Very few persons in my experience, though careful thinkers, realize that women with misguided impressions of sex really live according to a double standard which is equally destructive of social and moral stability as the man's double standard. The effect of their double standard is that soon rather than late, and in high rather than low degree, they violate the marriage contract, because they enter into it under the pretense of normal, complete love and then reveal themselves as bereft of natural physical attachment without which the whole marriage soon disintegrates. The single standard for woman is to decide *before* marriage that *all* its obligations are acceptable to her and then proceed to live happily with her husband according to them. Like all other contracts marriage does not permit 'change of mind.' "

The author is opposed to birth control, except for certain definite medical reasons. At the same time the book has much to commend it.

LOVE AND MORALITY. *An Attempt at a Physiological Interpretation of Human Thought.*
By Jacques Fischer. Alfred A. Knopf, Inc.
$3.50 5½ x 8, x + 291 *New York*

A strange speculation, which starts by elaborating the thesis that the combined lipoids of the brain provide the causal basis and mechanism for its intellectual activities, and ends with a biochemical defense of homosexuality. In between is a lot about sex and morality and some biochemistry. The book is certainly original and is well-written, but the central thesis of it all wants a great deal more evidence in its support than can now be adduced, before the author's wide-ranging deductions can be taken seriously.

BIOMETRY

MATHEMATICAL STATISTICS. *The Carus Mathematical Monographs No. 3.*
By Henry Lewis Rietz.
Open Court Publishing Co.
$2.00 5 x 7⅝; xi + 181 *Chicago*

An excellent little treatise, which puts its emphasis on the underlying mathematical theory of modern statistical methods rather more heavily than upon the practical applications and computations. It will, on this account, serve as a useful supplement to the elementary statistical manuals now in use.

A FIRST COURSE IN STATISTICAL METHOD.
By G. Irving Gavett.
McGraw-Hill Book Co., Inc.
$3.50 5¾ x 9; vii + 358 *New York*

An elementary textbook of statistics along conventional lines. Four appen-

dices deal with elementary mathematics. There is little that is original in the book. The sources cited are to a large extent second-hand. Mr. Yule's middle name appears as "Udney" throughout the book.

THE QUANTITATIVE METHOD IN BIOLOGY.
By Julius MacLeod.
Longmans, Green and Co.
$6.00 5⅜ x 8¾; xxiii + 228 *New York*

The second edition of an original and stimulating treatise, which discusses quantitative biology along quite unconventional lines. The biometrician will profit by reading this book, not for technique but for ideas.

PSYCHOLOGY AND BEHAVIOR

THE CASE FOR AND AGAINST PSYCHICAL BELIEF.
Edited by Carl Murchison.
Clark University
$3.75 6 x 9; 365 *Worcester, Mass.*

This is an entertaining book. Four kinds of people contribute to it. These are:

I. Those who are said to be "convinced of the multiplicity of psychical phenomena," which we take to be a hedging, professorial way of designating the worthy folk who swallow their spirits neat, raw, and without reservations as to time, place, or quantity. Here are found those doughty knights, Sir Oliver and Sir Arthur, and four others including, we blush to say, two ♀ ♀.

II. Those "convinced of the rarity of genuine psychical phenomena." Here are found McDougall, Driesch, Walter Franklin Prince, and F. C. S. Schiller. They like their spirits but are still moderate drinkers—the sort who claim to be able to "take it or leave it alone."

III. Those "unconvinced as yet." This has an ominous sound. The goblins will probably get them. There are two of these: John E. Coover and Gardner Murphy.

Finally, IV, are two staunch teetotallers, lips-that-touch-spirits-shall-never-touch-mine boys, who are "antagonistic to the claims that such phenomena occur." These two, of whom every scientific man should be proud, whether they are right or wrong, are Joseph Jastrow and the late, and greatly lamented, Harry Houdini.

The book is great fun, and the Clark University Psychology Department is to be congratulated for having staged so good a show.

SOCIAL PSYCHOLOGY INTERPRETED.
By Jesse William Sprowls.
The Williams & Wilkins Co.
$4.00 5¾ x 8½; xii + 268 *Baltimore*

This is a textbook for beginning students, written in the traditional mode of such books. The different theories of those who have discussed social psychology are expounded, charted in neat tables, and weighed against each other. But the "little red thread" is a very tenuous one indeed. About the only one we could find was that the author throughout regards it as impossible for individual behavior to be specifically distinguished from social behavior. It seems odd to find a book about social psychology in which neither Pareto nor Malinowski are mentioned, and in which there is no reference to William Graham Sumner's *Folkways*.

TIERSOZIOLOGIE. *Forschungen zur Völkerpsychologie und Soziologie, Band I.* *By Friedrich Alverdes.* *C. L. Hirschfeld* Mk. 4. 80 6¼ x 9½; viii + 152 *Leipzig* (paper)

This interesting volume fittingly opens a new series on folk psychology and sociology. The first four chapters are general discussions of animal associations; the reproduction of solitary animals; and social instincts in solitary animals. There then follows a long chapter giving the details regarding animal societies. With these data in hand the author proceeds to a general discussion of animal sociology and social psychology. There is a final short chapter on human social biology. There is a bibliography of four pages and an index. Altogether this is a useful addition to the literature.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

1st Book: THE ELECTRO-CHEMICAL FACTOR IN NEUROLOGY. *A Research in Electro Biology*, by *Ernest H. Pasqué.* *2nd Book:* NEW CONCEPTS OF PHYSICS, *by Calvin S. Page.*

The Atomic Research Assoc.
$10.00 5¾ x 9; 604 *Detroit*

The chief conclusions of the first of these two books bound together are:

"In a general résumé of the facts as compiled in this work, we can say this: The energy recognized as solar and planetary electro-magnetic force, under specific conditions, combines atoms according to definite laws, into combinations of molecules, protoplasms, and nuclei, which form the combinations known as cells.

"These cells, by reason of their atomic (chemic difference between nucleus and protoplasm) have in themselves opposite polarity. The prevailing electro-magnetic environment of the moment is the selector, or determining factor of such original combinations; this establishes cell pattern. Each pattern possessing its own atomic individuality, thus giving the cell its selective properties, which is the basis of its future development. The opposite polarity or potential difference, with electro-magnetic energy as the external exitor factor, causes the cells to generate sufficient electric energy to enable them to absorb new atomic combinations of such quantity and kind as they require to maintain, or increase this potential difference in order to sustain themselves or multiply."

"Life is an electrical phenomenon. The body as a whole, and its different organs, are power stations for specific work, and the nerves like wires, form a complicated, yet efficient network of communication between these organs. This network of communication is again equipped with sub-power stations, condensers, or tuners, to check, block, release, increase or transform the electricity flowing through them, and operating the motors of such organs as are concerned in the vital generating process."

The second book is about "Rx The Life Atom."

"Rx is the newly discovered kind of atomic matter whose atoms repel each other, upon contact, by their inherent, repulsion Energy.

"Rx is of all colors, governed by the associated atoms, and is not affected by the force of gravity as are all other known atoms. Hence Rx matter has no weight.

"The atoms of each kind of matter cohere to Rx atoms only, upon contact, by their own strength of inherent cohesion Energy."

Rx is held to have great therapeutic significance. Just what it will do and how it will do it seem a little vague, but there is an abundance of assertion that it will. On page 569 (near the end of the book) we find the following statement, which ought to be reassuring.

"Hence with this knowledge of Rx in the essential functions of organic nature it is self-evident that there must be great therapeutic value in the scientific application of light to the human body. I say scientific because the wonderful refinement of the harmonious operations of the cycles of animal life is not only evident in perfect health but in the universal constancy of the temperature of 98.6°."

STANDARD METHODS OF THE DIVISION OF LABORATORIES AND RESEARCH OF THE NEW YORK STATE DEPARTMENT OF HEALTH. *General Laboratory Procedures and the Methods Used in the Department for the Preparation of Media and Glassware; the Laboratories for Sanitary and Analytical Chemistry; the Research, Publications, and Library Department; the Antitoxin, Serum, and Vaccine Laboratories; the Diagnostic Laboratories; the Executive Offices.*

By Augustus B. Wadsworth.

The Williams & Wilkins Co.

$7.50 6 x 9; xx + 704 *Baltimore*

Dr. Wadsworth's laboratory in Albany is deservedly regarded as a model which marks the way of advance in public health laboratory work. It is a great service to have brought together in one volume a clear and detailed account of the organization of the Division of Laboratories and Research of the New York State Department of Health, and of the methods there used. This book will at once take rank as the standard reference work on laboratory technique for public health departments.

THE LION-HEARTED KITTEN *and other Stories.*

By Peggy Bacon. *The Macmillan Co.*

$2.00 5½ x 8½; 102 *New York*

This is an entertaining contribution to the Higher Biology. The drawings are superb. The tales which go with them are not quite so distinguished, but still there are high points, as, for example, the solemn discussion between the giraffe and the woodpecker, who had mistaken the former's neck for a tree trunk, as to whether the giraffe *was* a tree or not. This is a book to be read aloud in every biologist's home circle. It is suited to all ages.

ACUTE RHEUMATISM IN CHILDREN IN ITS RELATION TO HEART DISEASE. *Reports on Public Health and Medical Subjects No. 44.*

Ministry of Health.

H. M. Stationery Office

1s 6d. 6⅛ x 9¾; xii + 99 *London*

This is a report of a study by several officers of the British Ministry of Health on the bacteriology, incidence, and institutional treatment of acute rheumatism in children, considered in relation to the prevention of heart disease. It is a thorough piece of work of great interest to the student and the practitioner in the public health field.

INTRODUCTION TO THE HISTORY OF SCIENCE. *Vol. I. From Homer to Omar Khayyam. Carnegie Institution of Washington Publication No. 376.*

By George Sarton.

The Williams & Wilkins Co.

$10.00 7 x 10; xi + 839 *Baltimore*

The reputation of George Sarton in the field of the history of science has been firmly established by his journal *Isis*. We now have the first volume of what must for a long time be the master-work in the history of science, if it is completed along the lines laid down in this beginning. The ordinary man would be overwhelmed by the colossal nature of the task outlined. But Dr. Sarton cheerfully contemplates the preparation of *six more* volumes, each of the order of this one, as necessary to lay the *preliminary* foundations upon which alone a sound history of science may be written! May God spare him for his labor! For it is good. The present volume covers the period from Homer to Omar Khayyam, that is to say

up to the end of the eleventh century. The book is essentially an enormously thorough, detailed, and erudite bibliography, with pertinent and penetrating annotations. The subject is conceived so broadly that it will serve about equally well for a source book on the history of civilization, as on the history of science.